THE CARADOCIAN BRACHIOPOD FAUNAS OF THE BALA DISTRICT, MERIONETHSHIRE

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Pp. 327–471 ; 16 *Plates* ; 13 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 8 No. 7
LONDON: 1963

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 8, *No.* 7 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued November *Price Three pounds*

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By A. WILLIAMS

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SYNOPSIS

A study of the Caradocian brachiopods of the Bala district has shown that the majority are at least specifically distinct from their Shropshire contemporaries. Consequently the correlation between the rocks of North Wales and the Welsh Borderlands proved to be less certain than was anticipated. The differences appear to be accentuated by the existence of three distinct assemblages—the *Nicolella, Dinorthis* and *Howellites* associations—within the Caradocian

successions at Bala. Each association seems to have enjoyed its own optimum sedimentary environment which was rarely sufficiently widespread to enable species to flourish simultaneously in both regions. Detailed systematic analyses that led to this interpretation, are presented and involve the description of fifty-one species and subspecies, of which seventeen are new, belonging to thirty-five genera including the new ones—*Paracraniops*, *Rhactorthis* and *Cremnorthis*, and two new families are introduced.

I. INTRODUCTION AND ACKNOWLEDGMENTS

The shelly facies of the Bala district, Merionethshire, have played a part in the synthesis of Lower Palaeozoic Stratigraphy that is out of all proportion to their intrinsic worth because, having been described by Sedgwick (1845 : 7) as an important subdivision of his Cambrian System, they became the touchstone for both him (Sedgwick & M'Coy 1855 : xx) and Murchison (1854 : 7, 8) in furthering the merits of their respective systemic classifications. The ambiguity arising from this dual function survived even the objective pen of Lapworth who in his definition of the Ordovician system (Lapworth 1879) continued to use the " Bala Group " although, as he commented, the faunas were not as well known as those from Murchison's " Caradoc Formation ". This statement may seem surprising in face of the researches on Bala fossils conducted by such palaeontologists as M'Coy (1851 ; 1852), Salter and J. de C. Sowerby (see Sedgwick 1845 : 20) but the fact remains that their publications were mainly descriptive catalogues of collections recovered by a geologist who had already decided what the stratigraphical arrangement was. Actually, apart from certain aspects of Ruddy's studies (1897), it was not until 1922, when the late Dr. G. L. Elles published an account of the rocks to the south-east of Bala Lake, that field relationships and palaeontology were used concurrently to determine the faunal succession. One of the most important features of her work was the reiteration of Sedgwick's belief that the differences between the Upper and Lower Bala faunas, as typified by fossils from the Rhiwlas and " Bala " Limestones respectively, did not reflect so much a break as a change in emphasis (Elles 1922 : 164). This conclusion however was challenged by Bancroft (1928) in a brief but important paper which was the forerunner of some convincing demonstrations (1933 ; 1945) that shelly faunas can be used for detailed correlation of the Lower Palaeozoic rocks and that by doing so the succession at Bala can be shown to include only about one-half of the Caradocian of the Welsh Borderland and only the upper part of the Ashgillian of the Lake District.

By 1952 reconnaissance work had shown that there were discrepancies not only in Elles' map but also in the correlations afforded by Bancroft's recorded traverses. Since neither of them had examined the rocks to the north-east of the Lake, Dr. D. A. Bassett, Prof. H. B. Whittington and I decided to revise the stratigraphy of the entire district and at the same time to obtain large fossil collections with a view to re-examining the brachiopods and the trilobites, the principal elements of the Bala faunas. The aims of this joint undertaking have now been completed. The stratigraphical account, under triple authorship, together with a structural analysis by Dr. Bassett are being submitted to the Geological Society of London ; while the systematic revision of the trilobites conducted by Prof. Whittington, is being published by the Palaeontographical Society. These studies, including the one

presented below, are so dependent on one another and so completely complementary that no attempt has been made here either to enumerate entire fossil faunas or to give a stratigraphical account other than the outline required to illustrate the problems arising from correlations based on brachiopod assemblages : for such details the reader may refer to the papers just mentioned.

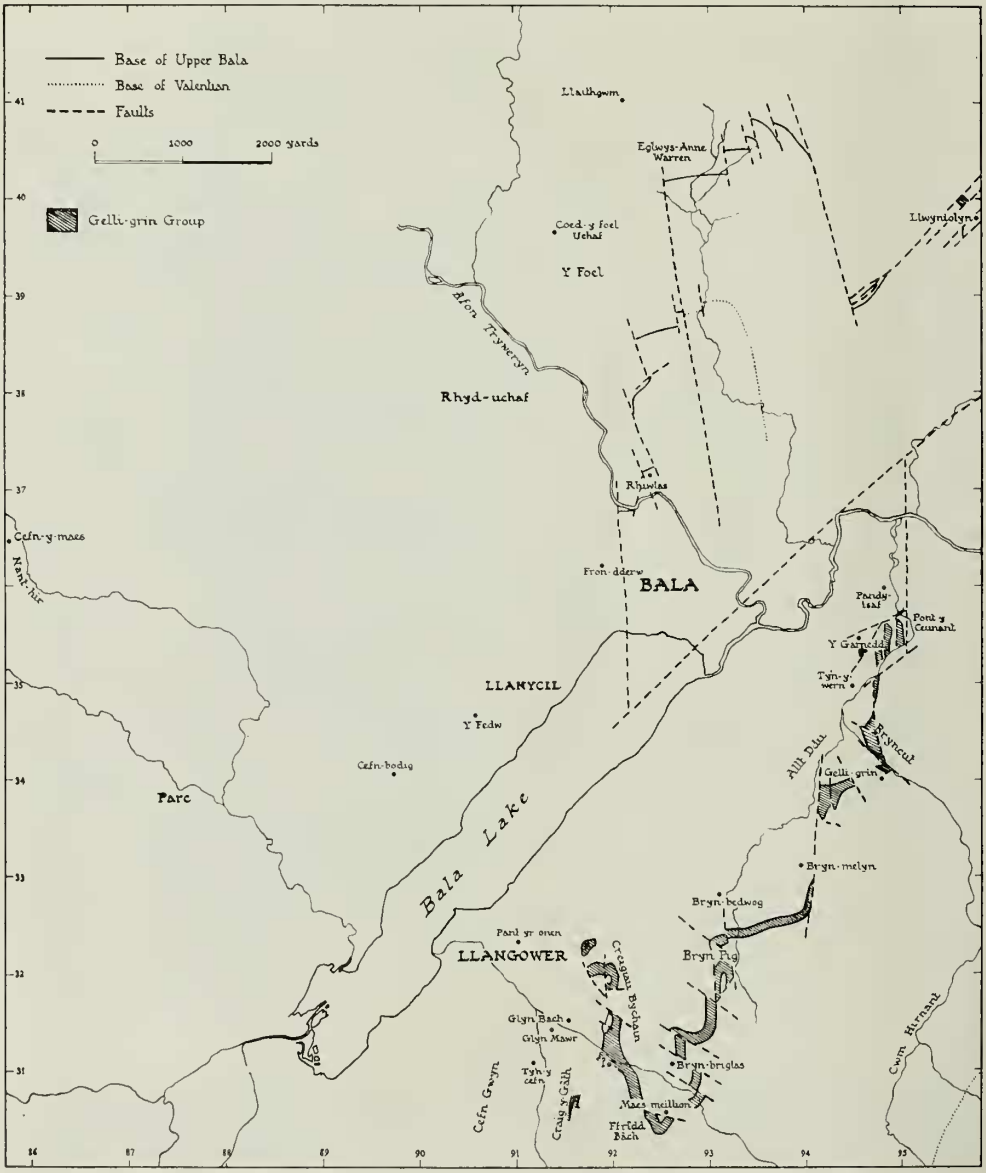

FIG. 1. Sketch map of the Bala District.

In order to be as objective as possible, the variability of brachiopod samples has been treated quantitatively according to the procedures adopted elsewhere (Williams 1962 : 69–79). Much of Bancroft's systematic work is, of course, quantitative in the sense that he used notations to describe the patterns of radial ornamentation in brachiopods or the distribution of pits in trinucleid trilobite brims. But he frequently ignored other morphological changes which are systematically at least as important as those he concentrated on ; and in any event, he never subjected his data to tests of significance so that his taxonomic treatment of samples tended to negate the precision of his methods. Consequently those species of his that may have been relevant to the identification of the Bala brachiopods have been re-investigated as critically as those proposed during the last century. Such comparative studies of samples from the Welsh Borderland and elsewhere have naturally provided a great deal of information and when the new data have led to a revision of our concept of an established species or to a more precise idea of its variability, an emended description of that species, even if it has not been found in the Bala district, has been included.

A host of friends from as far apart as Pasadena, Lund and Edinburgh have visited my colleagues and me during our field work and for pertinent observations here and recovered fossils there we express our appreciation in full confidence that they will not mind remaining anonymous. Special mention however, must be made of Mrs. Dorothy Whittington for her efficient taxi-service and her indefatigable collecting : without such aid we would have been working in the district yet. The brachiopod study itself has been greatly facilitated by access to large collections of topotypic material from the Welsh Borderland made by Mr. A. D. Wright and by the invaluable help in computation and photographic preparation of Miss Helen Lesser, research assistant in the Department of Geology at Queen's University : I am indeed indebted to them for their labours. Finally, it is a pleasure to record that specimens from the British and Sedgwick Museums were readily loaned by Dr. W. T. Dean and Mr. A. G. Brighton and that grants towards the cost of field work over these last ten years have been received from the University of Glasgow and the Queen's University, Belfast.

II. THE FAUNAL ASSEMBLAGES AND CORRELATION

Sixty-four species and subspecies of brachiopods, belonging to forty-two inarticulate and articulate genera, have been recovered from the Caradocian rocks of the Bala-Arenig district, Merionethshire. The succession consists essentially of about 4,500 ft. of mudstones and siltstones with minor ashes and sandstones and is poorly fossiliferous, except for the Gelli-grîn Group and parts of the Allt Ddu Group, so that the brachiopods recorded below as typical of the Derfel Limestone (see Whittington & Williams 1955) and the rest of the Nant Hir Group were collected from three and four localities respectively ; even the Glyn Gower list is based on collections from about a dozen exposures of the upper part of that Group. This sporadic occurrence of fossils is accentuated by their restriction mainly to bedding planes separated by variable thicknesses of sediments that have been disturbed by worm burrowings but are otherwise devoid of organic remains. Such bedding

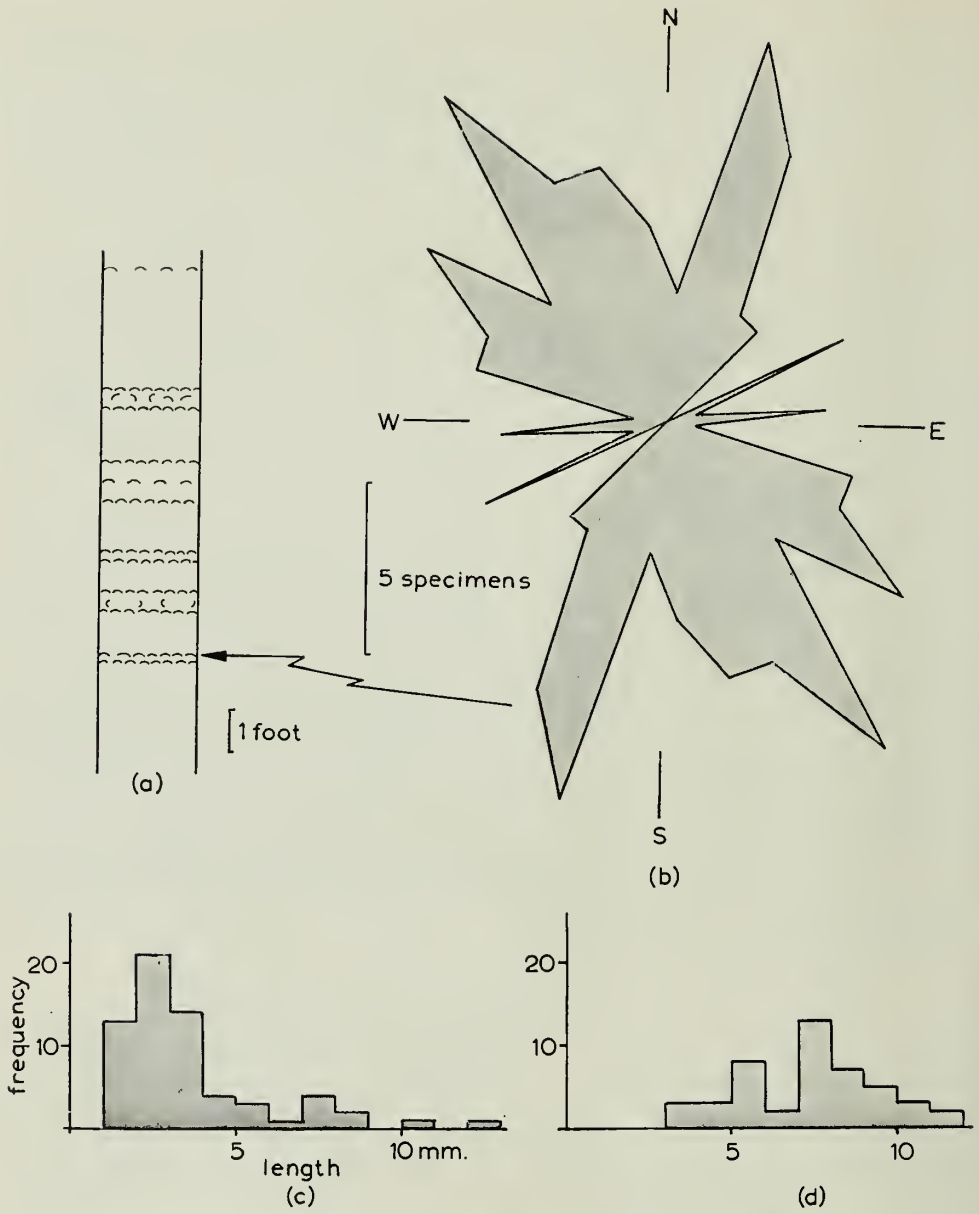

FIG. 2. Some data on the distribution of fossil brachiopods in the Caradocian sediments of Bala : (a) the occurrence of fossils (represented by small arcs) in 12 ft. 7 in. of Lower Allt Ddu siltstones exposed in the southern end of the roadside cutting south-west of Llanycil ; (b) the corrected orientations of the hinge-lines of 106 specimens of *Dinorthis berwynensis* (Whittington), *Heterorthis* cf. *retrorsistria* (M'Coy) and *Reuschella* cf. *horderleyensis* Bancroft taken from one bedding plane in the Lower Allt Ddu siltstones

planes are usually crowded with water-sorted assemblages so that the size-frequency distribution of most species from the coarser sediments tend to be strongly unimodal with a negative skew (Text-fig. 2). Yet, although shells are almost invariably disarticulated, both valves, even when they are quite dissimilar in shape, are well represented in any sample and are rarely broken or abraded. They show also the low degree of preferred orientation that one would associate with the winnowing of a community existing *in situ* rather than the accumulation of drifted remains (Text-fig. 2) ; and the fauna given below has been so interpreted as including the remnants of repeated colonizations of what was mostly an unfavourable environment for permanent occupation.

The distribution of the various species and subspecies is given in the following list in which

1, represents the Derfel Limestone at the base of the Nant Hir Group ;
2, the rest of the Nant Hir Group (species indicated by asterisks are the only ones recorded above the Cefn-y-maes horizon) ;
3, the Glyn Gower Group ;
4, the Lower Allt Ddu Group up to and including beds with *Dinorthis berwynensis* (Whittington) and *Heterorthis retrorsistria* (M'Coy) ;
5, the Middle Allt Ddu Group ;
6, the Upper Allt Ddu Group down to and including beds with *Howellites ultima* Bancroft ;
and 7, the Gelli-grîn Group.

	1	2	3	4	5	6	7
Anisopleurella multiseptata Williams	×	—	—	—	—	—	—
Bancroftina sp.	—	—	—	—	—	—	×
Bellimurina incommoda sp. nov.	—	—	—	—	—	—	×
Bicuspina spiriferoides (M'Coy)	—	—	—	×	—	×	×
Cremnorthis parva gen. et sp. nov.	—	—	—	—	—	—	×
Cyclospira sp.	—	—	—	—	—	—	×
Cyrtonotella aff. *kukersiana* (Wysogorski)	×	—	—	—	—	—	—
Dalmanella modica sp. nov.	—	—	—	—	—	—	×
Dalmanella sp.	—	—	×	×	—	—	—
Dinorthis berwynensis (Whittington)	—	*	×	×	—	—	—
Dinorthis berwynensis angusta subsp. nov.	—	—	—	—	—	×	×
Dolerorthis duftonensis prolixa subsp. nov.	—	—	—	—	—	—	×
Dolerorthis tenuicostata Williams	×	—	—	—	—	—	—
Dolerorthis sp.	—	—	—	—	—	×	—
Eoplectodonta lenis Williams	×	—	—	—	—	—	—
Eoplectodonta cf. *rhombica* (M'Coy)	—	—	—	—	—	—	×
Glossorthis sp.	×	—	—	—	—	—	—
Glyptomena cf. *osloensis* (Spjeldnaes)	—	—	—	—	—	—	×
Hedstroemina? spp.	—	×	×	—	—	—	—

south-west of Llanycil ; (c) the length-frequency distributions of 18 pedicle valves and 46 brachial valves of *Onniella* cf. *soudleyensis* (Bancroft) from the Nant Hir siltstones at Cefn-y-maes and (d) 18 pedicle valves and 28 brachial valves of *O. ostentata* sp. nov. from the Gelli-grîn Group.

Heterorthis cf. *retrorsistria* (M'Coy)	—	—	—	×	—	—	—
Hörderleyella sp.	×	—	—	—	—	—	—
Howellites intermedia Bancroft	—	—	—	—	×	—	—
Howellites antiquior (M'Coy)	—	—	—	—	—	—	×
Howellites striata Bancroft	—	—	—	×	×	—	—
Howellites ultima Bancroft	—	—	—	—	—	×	—
Howellites sp.	×	—	—	—	—	—	—
Kiaeromena cf. *kjerulfi* (Holtedahl)	—	—	—	—	—	×	—
Kiaeromena sp.	×	—	—	—	—	—	—
Kjaerina sp.	×	—	—	—	—	—	—
Kullervo aff. *panderi* (Öpik)	×	—	—	—	—	—	—
Leptaena ventricosa sp. nov.	—	—	—	×	—	×	×
Leptestiina derfelensis (Jones)	×	—	—	—	—	—	—
Leptestiina oepiki (Whittington)	—	—	—	—	—	—	×
Lingulella cf. *ovata* (M'Coy)	—	—	—	×	—	—	×
Lingulella cf. *tenuigranulata* (M'Coy)	—	—	—	—	—	—	×
Lingulella sp.	—	×	—	—	—	—	—
Macrocoelia prolata sp. nov.	—	—	×	×	×	×	×
Nicolella actoniae obesa subsp. nov.	—	—	—	—	—	—	×
Nicolella humilis Williams	×	—	—	—	—	—	—
Onniella aff. *avelinei* Bancroft	×	—	—	—	—	—	—
Onniella ostentata sp. nov.	—	—	—	—	—	—	×
Onniella cf. *soudleyensis* (Bancroft)	—	×	—	—	—	—	—
Orbiculoidea sp.	—	—	—	—	—	—	×
Orthambonites cessata sp. nov.	—	—	—	—	—	—	×
Oxoplecia mutabilis Williams	×	—	—	—	—	—	—
Oxoplecia sp.	—	—	—	—	—	—	×
Palaeostrophomena magnifica Williams	×	—	—	—	—	—	—
Paracraniops macella gen. et sp. nov.	—	—	—	—	—	—	×
Platystrophia precedens major Williams	×	—	—	—	—	—	—
Platystrophia cf. *sublimis* Öpik	—	—	—	—	—	—	×
Pseudocrania cf. *divaricata* M'Coy	—	—	—	—	—	—	×
Reuschella cf. *horderleyensis* Bancroft	—	*	×	×	×	—	—
Reuschella horderleyensis undulata subsp. nov.	—	—	—	—	—	×	×
Rhactorthis crassa gen. et sp. nov.	—	—	—	—	—	—	×
Rostricellula sparsa sp. nov.	—	—	—	—	×	×	—
Salopia salteri gracilis Williams	×	—	—	—	—	—	—
Salopia sp.	—	—	—	—	—	—	×
Sericoidea abdita Williams	×	×	—	—	—	—	—
Sericoidea sp.	—	—	—	—	—	—	×
Skenidioides cf. *costatus* Cooper	—	—	—	—	—	—	×
Sowerbyella musculosa sp. nov.	—	—	—	—	—	×	—
Sowerbyella sericea permixta subsp. nov.	—	×*	×	×	×	—	—
Sowerbyella sp.	×	—	—	—	—	—	—
Strophomena sp.	—	—	—	—	—	×	×
Vellamo sp.	—	—	—	×	—	—	—

The most important recent contribution to our understanding of the Caradocian shelly facies is undoubtedly that of Bancroft who, by using mainly morphological changes in the trinucleid trilobites and the dalmanellaceid and strophomenaceid brachiopods, effected a correlation of critical sections in England and Wales. The results of his studies are set out in a privately published paper (Bancroft 1933)

and again, with some emendation of his earlier conclusions (1945 : 181–186) ; they include the division of the Caradoc Series into seven stages based upon successions exposed in Shropshire, an arrangement that has been admirably reviewed by Dean (1958). The chief impression one gets from Bancroft's publications, apart from an appreciation of his ingeniously analytical use of morphological detail in separating species, is one of stratigraphical precision. There is a lavish use of zones complete with index fossils ; faunas of supposed correlative significance are recorded from sections often measured to the nearest inch : and discontinuities in the records of various stocks are filled in by linear interpolations between known occurrences. In effect, either as a consequence of his researches, or as a reflection of the principles by which he worked, his final paper (Bancroft 1945) is a striking confirmation of the ubiquity of fossil assemblages and the orthogenetic nature of evolution (see his accounts of the derivation of the dalmanellids and strophomenids, pp. 189–190, 202–203, etc.).

It is therefore not surprising to find that Bancroft experienced no difficulty in applying the stages of the standard successions in Shropshire to the Caradoc rocks of Bala (Text-fig. 3). Indeed, the only faunal difference he considered noteworthy (1945 : 247) is that *Kjaerina*, which is so characteristic of the Longvillian Stage of east Shropshire, becomes less common westwards and is unknown in north Wales. But complications are far greater than this sole comment suggests. Accepting for the moment his conclusion that the Caradocian rocks of Bala belong to the stages Harnagian to Longvillian inclusive, thirteen out of the forty-two genera found in them have not been recorded from their Shropshire correlatives (Dean 1958 : 193–231) and ten Shropshire genera within that stratigraphical range, including such important stocks as *Harknessella*, *Marionites* and *Smeathenella*, are absent from Bala. Moreover only a few specifically indeterminable moulds of *Bancroftina*, *Horderleyella*, *Hedstroemina* and *Kjaerina* have been recovered from the Bala sediments ; while another stratigraphically important stock, *Dalmanella*, which occurs only fairly often in the Gelli-grîn Group has proved specifically distinct from all other described forms (contrary to Bancroft's identification of it as *D. horderleyensis* (1945 : 193) and *D. indica* (1945 : 195)). In fact, only five out of the twenty-three genera found in both regions are at present known to be represented by conspecific forms. They are *Bicuspina spiriferoides* (Lower Longvillian), *Heterorthis retrorsistria* (Soudleyan), *Howellites antiquior* (Lower Longvillian), *Onniella* cf. *soudleyensis* (Soudleyan) and *Reuschella horderleyensis* (Soudleyan), all of which, according to Bancroft and Dean, have a restricted range in Shropshire (indicated by the stage name following each species).

The low proportion of species common to both areas requires some comment. Such widespread species might be inadequate for purposes of correlation because they may have been less susceptible to morphological change than, for example, *Dalmanella* or *Macrocoelia* and are therefore more likely to have a greater stratigraphical range. This is probably true of *B. spiriferoides* which occurs throughout the Allt Ddu and Gelli-grîn Groups in contrast to its brief appearance in Shropshire. On the other hand the proportion may be low because, although the Caradocian

brachiopod faunas of Shropshire are generally regarded as having been well studied, there are a surprising number of undescribed stocks including fifteen (Dean 1958: 218–225) that are at least congeneric with Bala contemporaries and these may ultimately prove to be more helpful for correlation than the so-called index fossils. In the meantime I am inclined to place a great deal of reliance on *H. antiquior* and *H. retrorsistria* both of which have such a restricted range in the Bala district that one is tempted to regard their incoming as coincident with their incursion into the Shropshire province. Two other species, first described from the Welsh

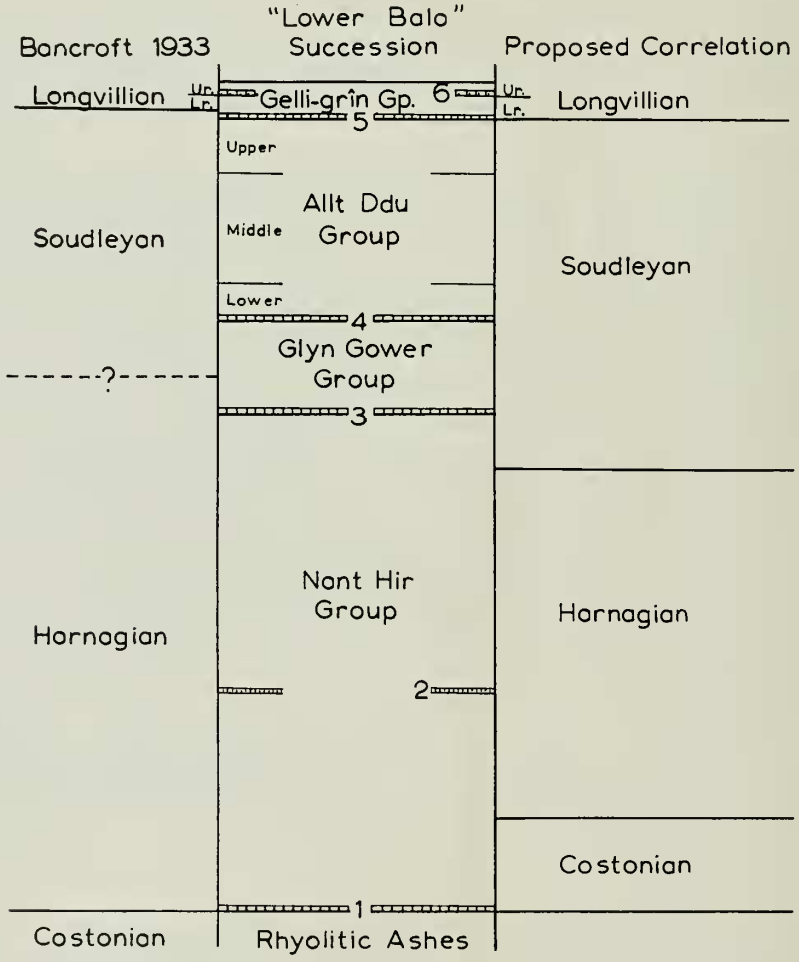

Fig. 3. The correlation of the Caradocian rocks of the Bala district according to Bancroft (1933) and the present study : 1, represents the Derfel Limestone ; 2, the fossiliferous horizon at Cefn-y-maes ; 3, the Cefn Gwyn Ash ; 4, the Frondderw Ash ; 5, the Pont-y-Ceunant Ash and 6, the Gelli-grîn Limestone.

Borderlands, namely *Dinorthis berwynensis* and *Leptestiina oepiki*, also have a fairly restricted occurrence in the Bala succession. The former is known from the Llanyblodwel beds of Montgomeryshire where, like its Bala relative, it is associated with *H. retrorsistria* ; the latter occurs in the Pen-y-garnedd Limestones that immediately succeed sandstones with an undoubted Lower Longvillian fauna (Whittington 1938*a* : 450). They confirm that the Upper Glyn Gower-Lower Allt Ddu Groups and the Gelli-grîn Group probably represent at least part of the Soudleyan and Lower Longvillian respectively. The location of the boundary between these two stages within the Bala succession is mainly a matter of convenience but since *Howellites antiquior* and *Leptestiina oepiki* appear first at the base of the Pont-y-Ceunant Ash, this member may be taken as the lowest constituent of the Longvillian. The base of the Soudleyan is even more indeterminate. A majority of the Nant Hir brachiopods was taken from a small thickness of mudstones about 1,700 ft. above the Derfel Limestone and only one of them, *Onniella* cf. *soudleyensis*, is at present also recorded in the rocks of the Welsh Borderlands. This species is found in the Soudleyan (Bancroft 1945 : 211) but the full ranges of early Caradocian *Onniella* are not well known and Professor Whittington's conclusion that the associated trilobites are on balance indicative of the Harnagian Stage, is more acceptable. The Harnagian-Soudleyan boundary is therefore probably somewhere above this horizon and may be taken as coincident with the first appearance of *Dinorthis berwynensis* and *Reuschella* cf. *horderleyensis*, i.e. just below the base of the Glyn Gower Group.

The correlation of the Derfel Limestone and the Upper Gelli-grîn ashes, which constitute respectively the base and the top of the Caradocian succession in the Bala area, is controversial for reasons that will become clear. On trilobite evidence, and particularly the presence of *Broeggerolithus* cf. *harnagensis* (Whittington 1955 : 420), the Derfel Limestone is usually regarded as being of Harnagian age. The large brachiopod fauna however, which is almost entirely unknown in Shropshire, is highly distinctive and is found in Anglesey in association with *Nemagraptus gracilis* and other diagnostic graptolites. Since this graptolitic fauna is too important to ignore, the basal member of the Nant Hir Group is best assigned to the Costonian stage.

The correlation of the terminal members of the Gelli-grîn Group has been affected by Bancroft's claim to have identified a widespread faunal break within the Longvillian. This is a recurrent theme in his papers. In 1933 he recorded a hiatus within the Lower ashes of the Gelli-grîn Group ; later (Bancroft 1945 : 185) he spoke of a " prolonged hiatus at the base of the [Upper Longvillian] substage " which he identified in the Bala district as coincident with the base of the Gelli-grîn Limestone ; and he implied in his discussion of the Caradocian faunas (pp. 182, 183) that there is palaeontological evidence for it. In order to show the size of this faunal break, the distribution and relative frequencies of the brachiopods found in the highest Caradocian rocks of Bala are given below where

1, represents the top of the Allt Ddu Group (twenty-one localities) ;

2, the Pont-y-Ceunant Ash (eight localities) ;

3, the lowest fifty feet of the lower calcareous ashes (twenty-five localities) ;

4, the middle part of the lower calcareous ashes with *Kloucekia apiculata* (M'Coy) (seventeen localities) ;

5, the lower calcareous ashes with *Chasmops* sp., immediately below the Gelli-grîn Limestone (six localities) ;

and 6, the upper calcareous ashes succeeding the Gelli-grîn Limestone (eight localities).

The letters indicating the frequency of various species have been compiled as a percentage occurrence in localities for each horizon with rare (r) denoting 0–25% occurrence, fairly common (fc) 26–50%, common (c) 51–75% and very common (vc) 76% or more. The species known from the Gelli-grîn Limestone at the type locality are prefixed by an asterisk.

	1	2	3	4	5	6
Bancroftina sp.	—	—	—	—	—	r
Bellimurina incommoda sp. nov.	—	—	r	r	fc	r
Bicuspina spiriferoides (M'Coy)	c	vc	c	fc	fc	r
Cremnorthis parva gen. et sp. nov.	—	—	—	—	—	r
Cyclospira sp.	—	r	r	r	—	—
**Dalmanella modica* sp. nov.	—	fc	fc	fc	fc	r
Dinorthis berwynensis angusta subsp. nov.	c	r	—	—	—	—
**Dolerorthis duftonensis prolixa* subsp. nov.	—	—	fc	c	vc	vc
Dolerorthis sp.	r	—	—	—	—	—
**Eoplectodonta* cf. *rhombica* (M'Coy)	—	vc	vc	c	c	vc
Glyptomena cf. *osloensis* (Spjeldnaes)	—	—	—	—	r	—
Howellites antiquior (M'Coy)	—	c	vc	vc	vc	r
Howellites ultima Bancroft	vc	—	—	—	—	—
Kiaeromena cf. *kjerulfi* (Holtedahl)	r	—	—	—	—	—
**Leptaena ventricosa* sp. nov.	c	c	fc	fc	c	r
**Leptestiina oepiki* (Whittington)	—	r	r	fc	vc	fc
Lingulella cf. *ovata* (M'Coy)	—	—	—	r	—	r
Lingulella cf. *tenuigranulata* (M'Coy)	—	—	—	r	—	—
Macrocoelia prolata sp. nov.	c	fc	fc	r	—	fc
**Nicolella actoniae obesa* subsp. nov.	—	r	fc	fc	c	vc
Onniella ostentata sp. nov.	—	fc	r	r	—	r
Orbiculoidea sp.	—	—	—	—	—	r
Orthambonites cessata sp. nov.	—	—	r	r	—	—
Oxoplecia sp.	—	—	r	—	—	—
Paracraniops macella gen. et sp. nov.	—	—	r	r	—	—
Pseudocrania cf. *divaricata* M'Coy	—	—	r	—	—	—
Platystrophia cf. *sublimis* Öpik	—	fc	r	r	—	—
Reuschella horderleyensis undulata subsp. nov.	vc	c	fc	r	—	c
Rhactorthis crassa gen. et sp. nov.	—	—	—	r	r	r
Rostricellula sparsa sp. nov.	r	—	—	—	—	—
Salopia sp.	—	r	—	—	—	—
Sericoidea sp.	—	—	—	—	—	r
**Skenidioides* cf. *costatus* Cooper	—	r	fc	fc	fc	r
Sowerbyella musculosa sp. nov.	fc	—	—	—	—	—
Strophomena sp.	—	—	r	r	fc	—

From the list, it is clear that the so-called break at the base of the Gelli-grîn Limestone does not exist and that although ten new species were introduced into the area during the deposition of the Pont-y-Ceunant Ash, important remnants of the Upper Allt Ddu fauna persisted and even more new species appeared within the lower calcareous ashes. As far as correlation is concerned the brachiopods are singularly unhelpful. Seventeen out of the twenty-eight genera found in the Gelli-grîn Group have not been recorded from either substage of the Shropshire Longvillian and only the sudden rarity of *H. antiquior* in the upper calcareous ashes, after its prolific occurrence in the lower beds, suggests that the youngest members of the Gelli-grîn Group belong to the Upper Longvillian.

The most disappointing aspect of this study is the failure to identify detailed subdivisions of the Shropshire Caradocian in an area that is only fifty miles distant. Indeed the differences between the two brachiopod faunas are so profound that even the use of the stages proposed by Bancroft calls for a number of compromises and the possibility that we are really comparing the fossil remnants of what were once two distinct benthic provinces must now be considered.

The most obvious feature of the brachiopod faunas recovered from the Caradocian rocks of Bala is the relative richness of the Derfel Limestone and Gelli-grîn assemblages. Between them they include all but four of the genera recorded in the district and the exceptions—*Hedstroemina*, *Heterorthis*, *Rostricellula* and *Vellamo*—together with twelve other genera are all that are found in the intervening four thousand feet of strata. There is also some relationship between these two assemblages in that certain genera, *Dolerorthis*, *Eoplectodonta*, *Leptestiina*, *Nicolella*, *Oxoplecia*, *Platystrophia* and *Salopia*, are common to them both but unknown from the rest of the succession, while *Onniella* and *Sericoidea* are additionally recorded only from the Nant Hir. Not one of these recurring genera however, is represented by the same species and if the two assemblages indicate briefly occurring intrusions into the Bala environment of a fauna belonging to another province, then the composition of that fauna changed generically as well as specifically during the intervening period. Thus *Anisopleurella*, *Cyrtonotella*, *Glossorthis*, *Horderleyella*, *Kjaerina*, *Kullervo* and *Palaeostrophomena* are limited to the Derfel Limestone ; while *Bellimurina*, *Cremnorthis*, *Cyclospira*, *Glyptomena*, *Orthambonites*, *Paracraniops*, *Pseudocrania*, *Rhactorthis*, *Skenidioides* and *Strophomena* are exclusive to the Gelli-grîn Group. The most intriguing aspect of such a fauna is its strong Baltic affinities (Whittington & Williams 1955 : 398–402) and it is proposed to refer to it as the *Nicolella* association on the understanding that its principal elements are those stocks common to both the Derfel Limestone and the Gelli-grîn Group, supplemented by less persistent associates like those listed above but excluding at least *Sericoidea* and *Onniella*.

The remaining genera, limited though they are in numbers, also show some interesting relationships. *Dinorthis*, *Macrocoelia* and *Reuschella*, with rare *Dalmanella* and *Hedstroemina*, first appear in the Glyn Gower Group and these three, except for the absence of *Dinorthis* from the Middle Allt Ddu and its disappearance just above the base of the Pont-y-Ceunant Ash, thereafter persist throughout the Caradocian successions of the Bala district. Just above the Frondderw Ash these

stocks are joined by *Heterorthis*, which occurs in brief profusion, *Leptaena* and *Bicuspina*, both of which reappear in the Upper Allt Ddu to continue through into the Gelli-grîn Group. *Dinorthis*, *Leptaena*, *Heterorthis* and *Bicuspina* then were subject to vacillating occurrences within the Caradocian succession in the manner of the *Nicolella* association and may be referred to as the *Dinorthis* association : the genera *Heterorthis* and *Bicuspina*, are known from the Llandeilian rocks of Bohemia. A third association remains to be described ; it includes *Howellites*, which first appeared in the Derfel Limestone but is pre-eminently characteristic of the Allt Ddu and Gelli-grîn Groups, *Sowerbyella* which occurs throughout all Groups except the Gelli-grîn, and rare ancillary members like *Rostricellula*. The *Howellites* association to which *Macrocoelia* and *Reuschella* are more appropriately relegated, is interesting in that the ancestral stocks of its members are known from the pre-Caradocian rocks of the Anglo-Welsh area and it may therefore be regarded as the chief indigenous group in the Bala assemblages.

Whether these three associations represent remnants of biotic communities that existed in a north Welsh province during Caradocian times is a matter for further exploration. Their heterogeneity at first seems to be against it. The simultaneous appearance of *Leptestiina*, *Nicolella*, *Platystrophia*, etc. at the base and the top of the Caradocian succession in the Bala district is noteworthy and although they occur with different stocks and as distinct species, such differences can reasonably be attributed to replacement and speciation during the intervening period. *Howellites* and *Sowerbyella* however, the two principal members of the supposed indigenous association which occur throughout the Allt Ddu Group, can be referred to five species, *H. striata*, Bancroft, *H. intermedia* Bancroft and *H. ultima* Bancroft, *S. sericea permixta* subsp. nov. and *S. musculosa* sp. nov. Had the collections examined been samples of an evolving community in continuous occupation of the Allt Ddu silts, specific differences would have been expected to arise phylogenetically like the change in radial ornamentation of *Howellites* described by Bancroft (1945 : 204). In fact those trends proved not to be valid, and, when the variability of other characters is taken into account, there are better reasons for believing the three *Howellites* species to have been contemporary stocks, each in turn playing its part in a continual colonization of the silty environment then extant. Similar relationships exist between the two *Sowerbyella* species. *S. sericea permixta* persisted throughout the Nant Hir and Glyn Gower Groups into the Allt Ddu but was replaced by the unrelated *S. musculosa* towards the top of that Group.

Even within associated generic stocks therefore, there seems to be good evidence for replacement and transposition at the specific level. None the less it is probably significant that the *Nicolella* association is found in the only two suites of calcareous sediments within the Bala succession, whereas the *Dinorthis* and *Howellites* associations are pre-eminently characteristic of the sandier and muddier beds respectively.

The existence of such facies controls can, to some extent, be demonstrated in the following manner. Fifty-seven genera of brachiopods have been recorded from the Caradocian deposits of England and Wales ranging in lithology from limestones to mudstones and conglomerates. Ignoring the genera *Bancroftina*, *Dolerorthis*,

Lingulella, *Macrocoelia* and *Sowerbyella*, which have been taken from every kind of sediment, and *Anisopleurella*, *Bellimurina*, *Cremnorthis*, *Cryptothyris*, *Cyclospira*, *Cyrtonotella*, *Glossorthis*, *Glyptorthis*, *Heterorthina*, *Kiaeromena*, *Kjerulfina*, *Kullervo*, *Marionites*, *Orthambonites*, *Orthorhynchula*, *Palaeostrophomena*, *Paterula*, *Philhedra*, *Pseudocrania*, *Ptychoglyptus*, *Skenidioides* and *Triplesia* which are at present known only from one particular horizon in one area, a residuum of twenty-nine genera is left. The incidence of species belonging to these genera in six different lithologies is given below where :

1, represents limestones ;
2, calcareous sandstones ;
3, sandstones and grits ;
4, siltstones ;
5, mudstones and shales ;
and 6, calcareous mudstones.

The data have been compiled from the papers of Bancroft (1933, 1945), Whittington (1938, 1938*a*), Dean (1958, 1959) as well as from the present study so that there is a fairly wide coverage of both lithology and locale : and a clear preponderance of species for any one genus in a particular lithology is indicated by an asterisk.

	1	2	3	4	5	6
Bicuspina	—	×	*	×	—	×
Dalmanella	—	*	×	×	×	×
Dinorthis	—	×	*	×	×	×
Eoplectodonta	—	×	—	×	—	*
Harknessella	×	×	×	×	—	—
Hedstroemina	—	—	—	*	—	—
Heterorthis	×	×	*	×	—	×
Horderleyella	—	×	*	×	—	×
Howellites	—	×	×	*	×	—
Kjaerina	×	*	—	×	×	×
Leptaena	—	*	*	×	—	×
Leptestiina	—	×	—	×	—	*
Nicolella	×	×	—	×	—	*
Onniella	—	×	—	×	*	×
Orbiculoidea	×	*	×	×	—	×
Oxoplecia	—	×	×	×	—	×
Paracraniops	—	—	—	×	×	*
Platystrophia	×	×	—	×	—	*
Reuschella	—	×	×	×	×	×
Rhactorthis	—	*	—	×	—	×
Rostricellula	—	—	*	×	—	—
Salopia	—	×	×	×	—	×
Schizocrania	×	—	—	×	×	×
Sericoidea	—	—	—	×	*	×
Siphonotreta	—	×	×	×	—	—
Smeathenella	—	×	×	×	—	—
Strophomena	×	×	—	×	—	*
Trematis	×	—	—	×	×	×
Vellamo	—	—	×	*	—	—

Most of the genera are obviously tolerant of many lithological environments, a reflection no doubt of species adaptation, but some of the patterns are worth noting. The preferred environment is undoubtedly the silty bottom which supported species of every genus listed. *Onniella*, *Sericoidea* and *Paracraniops* are especially characteristic of the muddy environment : but above all, the list confirms the prevalence of the *Nicolella* association (with *Eoplectodonta*, *Leptestiina*, *Platystrophia*, *Rhactorthis*, and *Strophomena*) in a lime-rich environment and of the *Dinorthis* association (with *Bicuspina*, *Dalmanella*, *Heterorthis* and *Leptaena*) in a sandy substratum. In this context the diachronism of faunas, implicit in Bancroft's correlations, is to be expected. Thus the *Nicolella* association appeared during Lower Longvillian times in the Bala district, in Upper Longvillian times in the Berwyn Hills, but not until Marshbrookian-Actonian times in South Shropshire. In contrast, the *Dinorthis* association, with the possible exception of *Bicuspina*, is present in the sandy Costonian facies of Shropshire but did not reach the Bala region until Soudleyan times when the coarser Glyn Gower beds were being deposited.

III. SYSTEMATIC DESCRIPTIONS

OBOLACEA King 1846

OBOLIDAE King 1846

LINGULELLINAE Schuchert 1893

LINGULELLA Salter 1866

TYPE SPECIES. *Lingula davisii* M'Coy by subsequent designation of Dall (1870 : 159).

Lingulella cf. *ovata* (M'Coy)

(Pl. 1, figs. 1–3)

The impressions of a few lingulids have been recovered from the Caradoc rocks of the Bala district, especially from those assigned to the Gelli-grîn Group, and the external and internal moulds of a pedicle valve, (BB.28985–86) from coarse calcareous ashes exposed 400 ft. east-south-east of Bryn-briglas Farm, have been figured to illustrate their close resemblance to *Lingulella ovata* (M'Coy 1846 : 24). The valve, which was 18 mm. long, 11·5 mm. wide and about 3 mm. deep, was elongately oval in outline with subparallel lateral margins and evenly convex in longitudinal and transverse profiles. The external surface was ornamented by closely set, fine, raised, concentric ridges grouped at about 6 to 7 per mm. at 10 mm. antero-medianly of the umbo. The postero-median area is not well preserved and no details of the ventral interior around the beak are known, but another internal mould of a dorsal valve (BB.28987), from calcareous ashy mudstones of the Gelli-grîn Group exposed above the limestone in the old quarry 500 ft. west-south-west of Gelli-grîn Farm, which can probably be allocated to the same stock, shows the trace of a short median ridge extending anteriorly from the umbonal region for about 5 mm.

In outline and ornamentation the specimens are certainly very like *L. ovata*, and although the pedicle valve may prove to be significantly deeper, more material will have to be obtained to determine whether this difference is systematically important.

CRANIACEA Gray 1840
CRANIIDAE Gray 1840
Pseudocrania M'Coy 1851

TYPE SPECIES. *Crania antiquissima* Verneuil by original designation of M'Coy (1851 : 387).

Pseudocrania* cf. *divaricata M'Coy
(Pl. 1, figs. 4, 5 ; Text-fig. 4)

Deformed external and internal moulds, about 21 mm. long, of a brachial valve (BB.28988–89), of *Pseudocrania* have been collected from calcareous ashes of the Gelli-grîn Group exposed immediately west of the fence at the south-east end of the Rhiwlas Limestone scarp, about 500 ft. south-west of B.M.1338.7, Bryn Pig. The exterior of the valve was gently convex, about one-tenth as deep as long with the apex located near the straight posterior margin ; the anterior part of the commissure was slightly emarginate. The surface of the external mould is not well preserved but here and there, especially peripherally, there occur impressions of radiating, rounded costellae numbering about 3 per mm. In contrast, the fine details of the internal mould permit a full reconstruction of the dorsal musculature and the mantle (Text-fig. 4). The elliptical anterior adductor scars, inserted on either side of a low median ridge about half way along the valve from the posterior margin, are the most conspicuous muscle set in the manner typical of *Pseudocrania*. Anteriorly and antero-medianly to them, on a slightly raised triangular platform, occur respectively a rather widely spaced pair of elevator scars and a smaller subjacent pair of protractor scars. The unpaired median muscle occupied a small depression which indented the thickened posterior margin to the valve, and lateral to it the posterior adductor and the oblique internal scars can be made out. The pallial sinus pattern within the mantle appears to have consisted of a pair of *vascula media* which branched into three main canals as they emerged from the visceral chamber anterior of the anterior adductor bases, and a pair of arcuate, highly branched *vascula genitalia* originating lateral of the posterior adductors.

The specimens are very close in morphology to those figured by Davidson (1866, pl. 8, figs. 7–12) as *Crania divaricata* (M'Coy) and especially to a dorsal internal mould from the Chair of Kildare (pl. 8, fig. 11*a*) which also possesses the impression of a triangular platform in front of the anterior adductor impressions. Indeed the only noteworthy contrast is the relatively small size and shallowness of the posterior adductor impressions of the Welsh internal mould, and until more is known about the systematic importance of this difference, the moulds are best compared with M'Coy's species.

Family CRANIOPSIDAE nov.

Subequivalve, unattached craniaceids (?) usually with well defined platforms of secondary shell substance bearing muscle impressions ; shell substance impunctate.

Genus *PARACRANIOPS* nov.

Diagnosis. Oval, subequivalve shells with apices of both valves located at or near posterior margins ; external surfaces ornamented by well developed but sporadically occurring lamellae eccentric about apices of valves ; ventral (?) interior with subcircular to subtriangular raised area culminating in low eminence posteriorly but broken anteriorly by median depression, that possibly accommodated the oblique internal muscle bases, and containing anteriorly a pair of suboval impressions, interpreted as scars of anterior adductors; elongate impressions outside

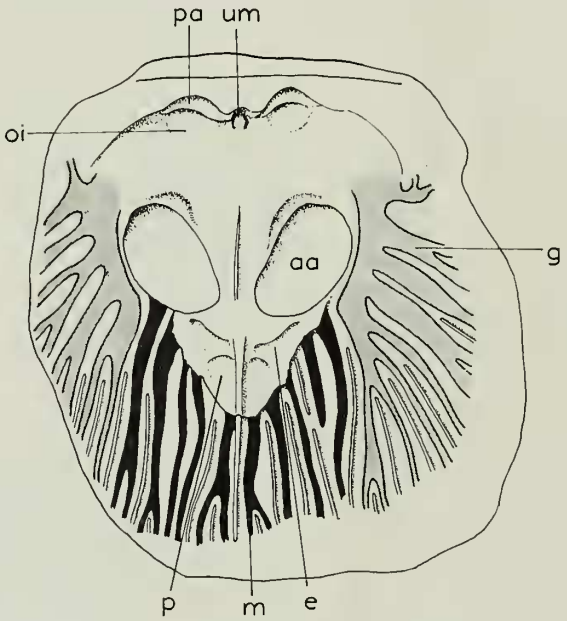

Fig. 4. An interpretation of the impressions found in the dorsal interior of *Pseudocrania* cf. *divaricata* M'Coy, ×3·5 approx.: *aa*, anterior adductor scar ; *e*, elevator scar ; *g*, *vascula genitalia* ; *m*, *vascula media* ; *oi*, oblique internal scar ; *p*, protractor scar ; *pa*, posterior adductor scar ; *um*, unpaired median scar.

postero-lateral flanks of raised area probably represent posterior adductors ; dorsal (?) interior with pair of low ridges commonly widely splayed about small, postero-median eminence, narrowly elongate indentations parallel with and posterior to ridges, and pair of larger, suboval, impressions antero-lateral to them and separated by broad median band probably represent dorsal posterior and anterior adductor scars respectively ; shell substance calcareous, impunctate.

TYPE SPECIES. *Craniops ? pararia* Williams (1962) from the Kiln Mudstones, Craighead.

DISCUSSION. When the species *Craniops ? pararia* was first described (Williams 1962 : 88) it was pointed out that the internal morphology was so different from that of *C. squamiformis* (Hall), the type species of *Craniops*, or any other Silurian and Devonian stock that its inclusion in the genus *Craniops* was only provisional. Since then additional material from Craighead and also internal and external moulds from the Bala district have shown that the differences are indeed important.

The chief difficulty in assessing the taxonomic importance of morphological changes in extinct fossil groups arises from the uncertainty over their anatomical significance and the craniopsids, lacking as they do any obvious affinities with other, better known brachiopods, are no exception. Cooper (1956 : 236) has classified them as trimerellaceids, and included them in the Paterulidae. In the Russian Treatise on Brachiopoda (Gorjansky 1960 : 177), they have been assigned to the craniaceids. This allocation seems preferable because they do bear some resemblance to certain free-living craniids like *Pseudocrania* in the lack of a pedicle opening and

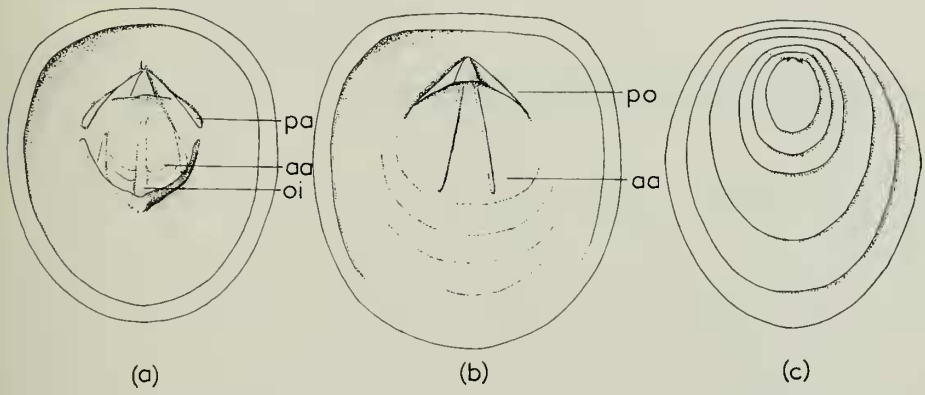

FIG. 5. The ventral ? (a) and dorsal ? (b) interiors and dorsal exterior (c) of *Paracraniops pararia* (Williams), ×5 approx.: *aa*, anterior adductor scar ; *oi*, oblique internal scar ; *pa*, posterior adductor scar ; *po*, posterior adductor and oblique internal scars.

in the possession of a calcareous shell, although both these characters could well have arisen independently ; and the absence of caeca penetrating the shell in the manner of the craniaceids may reflect such a process. None the less there are certain indentations on the floors of both valves that can confidently be taken as the scars of muscle attachments (Text-fig. 5). Two well-defined pairs in both valves probably represent the seats of attachment of the adductor bands, and, provided the apices of the valves point posteriorly, may be homologized with the posterior and anterior sets of the craniaceids. In addition to these, the more elaborate platform of one of the valves, is deeply indented antero-medianly and if this is the area once occupied by the oblique internal muscles then this valve is the " ventral " or " pedicle " and its counterpart the " dorsal " or " brachial ". If this is so, the elongate impressions

lying posterior to the ridges in the dorsal valve may represent the seats for the dorsal ends of the oblique internal muscles as well as the posterior adductors. For this reason alone the designation of the valves is the reverse of that put forward previously (Williams 1962) but it is still, of course, a matter of inference and cannot be accepted with certainty.

Having orientated the shell it is now possible to discuss the difference among the new genus, *Craniops* Hall 1859 (*Pholidops* Hall 1859 is a junior homonym) and *Pseudopholidops* Bekker 1921 which relate entirely to internal features. In the ventral (?) valve of *Craniops*, a central subtriangular platform pointing anteriorly is well developed so that the raised antero-median ridge, presumably for the reception of the ventral ends of the oblique internal muscles, contrasts with the median indentation, within the differently shaped raised area, of the new genus. The ventral posterior adductor scars are also differently located for in *Craniops* they are so widely separated as to form conspicuous, subcircular impressions at the ends of the base to the main platform. In the dorsal (?) valve the differences are even more striking because an elaborate platform containing both sets of adductor scars is characteristic of *Craniops* in contrast to the pair of widely divergent ridges separating the two adductor sets as in *Paracraniops*.

The species included by Bekker (1921 : 64–66) within his genus *Pseudopholidops* have a variable internal morphology but are immediately distinguishable from those assigned to *Paracraniops* in possessing three discrete pairs of muscle scars in the dorsal valve. Only one ventral interior has been described, that of *Pseudopholidops complicata* Bekker (1921 : 66), but this is also quite different in the extreme posterior location of the posterior adductors and also in the presence of a split ridge postero-medianly.

Apart from the type species, *Craniops trentonensis* (Hall 1866), *Craniops minor* (Winchell & Schuchert 1893), *Craniops attenuata* Cooper 1956 and *Craniops tenuis* Cooper 1956, all from Mohawkian rocks of N. America, probably belong to the new genus, although at present the interiors of these species are unknown. *Paracraniops macella* sp. nov. from the Caradocian rocks of Bala and " *Pholidops* " *infrasilurica* Huene 1899, *P. estona* Bekker 1921 and *P. elegans* Bekker 1921 from the mid-Ordovician of the Baltic region are only provisionally included because they differ from the Scottish and American stocks in the terminal location of the apices of the valves and also in the absence of the postero-median eminence in the dorsal valve.

Paracraniops macella gen. et sp. nov.
(Pl. 1, figs. 6–8)

Diagnosis. Elongately oval subequivalve *Paracraniops* with valves just over three-quarters as wide as long measured between a slightly flattened posterior margin and a strongly curved anterior one, ventral (?) valve slightly more convex, apices acute terminal ; lamellose ornamentation strongly developed, becoming widely spaced antero-medianly ; ventral (?) interior with subcircular platform, less than two-thirds as long as valve, containing antero-laterally a pair of suboval adductor impressions and broken antero-medianly by a long depression presumably

the median oblique internal scar, posterior adductors elongate, flanking low posterior edges of platform ; dorsal (?) interior with poorly developed ridges widely extended about a low posterior eminence, anterior adductor scars impressed antero-laterally within a vaguely defined raised border extending anteriorly for about one-half the length of the valve.

		length	width (mm.)
Holotypes.	Internal mould of ventral (?) valve (BB.28990)	2·0	1·5
Paratypes.	External mould of ventral (?) valve (BB.28991)	1·7	1·4
	External mould of dorsal (?) valve (BB.28992)	1·8	1·3
	Internal mould of dorsal (?) valve (BB.28993)	1·8	1·4
	External mould of ventral (?) valve (BB.28994)	1·5	1·0
	External mould of dorsal (?) valve (BB.28995)	1·9	1·5
	Internal mould of dorsal (?) valve (BB.28996)	2·0	1·5

Horizon and locality. Calcareous ashes of the Gelli-grîn Group exposed in a quarry at the side of the road leading to Y Garnedd, about 300 ft. south-east of that farm.

Discussion. The moulds collected from the Gelli-grîn Group may be separated immediately from Scottish and American *Paracraniops* in the terminal location of the apices of the valves although in this respect it resembles specimens described by Bekker (1921 : 62, pl. 2, figs. 4, 5) as *Pholidops estona*. Both stocks are also elongately oval but the new species may prove to be relatively wider (see Table 1) for the measurements given by Bekker suggest that *P. estona* was less than three-fifths as wide as long. The average length of the platform relative to the length of 4 ventral valves from Bala was 56·3% (variance 8·33) and, judging from Bekker's illustration, the ventral muscle platform of *P. estona* is similarly proportioned although within the anterior margin there also occurs a pair of curved ridges extending parallel with the margin from a central ring of shell, a structure not impressed in the Welsh moulds. In the dorsal interior of *P. estona* the anterior adductor scars are very much smaller and the posterior ridges are not obtusely splayed as in *Paracraniops macella*.

Table 1

$\bar{l}$ mm. (var. l) . . .	1·68	(0·123)
$\overline{w}$ mm. (var. w) . .	1·29	(0·091)
r . . .	0·937	
a (var. a) . . .	0·8602	(0·00821)

Table 1. Statistics of maximum length (l) from posterior to anterior margins and maximum width (w) of 13 ventral (?) valves of *Paracraniops macella* sp. nov.

Superfamily ACROTRETACEA Schuchert 1896

Family DISCINIDAE Gray 1840

Genus ***ORBICULOIDEA*** D'Orbigny 1847

TYPE SPECIES. *Orbicula forbesii* Davidson 1848 (application pending under the Plenary Powers (*Bull. Int. Comm. Zoo. Nomencl.*, **19**, No. 5 [in Press]) : appeal by A. J. Rowell).

Orbiculoidea sp.

(Pl. 1, fig. 9)

The interior of an incomplete brachial valve (BB.29135), taken from calcareous ashes exposed above the Gelli-grîn Limestone in the old quarry just north of the track and 500 ft. west of Gelli-grîn Farm, is all that has been found of the genus *Orbiculoidea* in the Caradocian rocks of Bala. The valve is eccentrically conical about an apex which is situated 1 mm. forward of the straight posterior margin, although it tends to flatten out about 2·5 mm. anterior of the apex. Judging from details of the interior, the external surface was ornamented by fine, closely spaced, concentric ridges and the valve was probably subcircular in outline. The only other internal feature worth noting is a faint, thin ridge extending antero-medianly from the apex for about 1 mm.

Undescribed *Orbiculoidea* are known throughout much of the Caradocian of Shropshire (Dean 1958 : 218–222) and the Bala form may prove to be related to them, but more material will have to be obtained for any conclusive comparative study.

Superfamily ORTHACEA Woodward 1852

Family ORTHIDAE Woodward 1852

Subfamily ORTHINAE Woodward 1852

Genus ***ORTHAMBONITES*** Pander 1830

TYPE SPECIES. *Orthambonites transversa* Pander by subsequent designation of Dall (1877 : 51).

Orthambonites cessata sp. nov.

(Pl. 1, figs. 10–14)

DIAGNOSIS. Unequally biconvex subquadrate *Orthambonites* with high pedicle valve about one-third as deep as long and curved apsacline, ventral interarea almost one-quarter as long as valve ; brachial valve obscurely sulcate, over two-thirds as long as wide and nearly one-quarter as deep as long, dorsal interarea strong, curved anacline ; ornamentation consisting of about 15 subangular costae about 0·5 mm. in wavelength, 5 mm. anterior of the ventral umbo with delicate concentric lamellae ; strong teeth supported by receding dental lamellae, ventral muscle field subtriangular in outline about three-tenths as long as pedicle valve with pair of adductor scars,

not enclosed by diductor scars ; ventral pallial sinus pattern saccate, *vascula media* separated at their confluence with diductor submedian lobes by boss of secondary shell in adult shells ; cardinal process massive but undifferentiated, brachiophores extending antero-ventrally for less than one-quarter the length of brachial valve, as pair of divergent blades, rectangular in outline, sockets oval and deep, defined by secondary shell surrounding bases of brachiophores, median ridge strong, dorsal adductor field quadripartite, extending forward of dorsal umbo for over one-half the length of brachial valve and including subequal posterior and anterior adductor scars ; dorsal pallial sinus pattern poorly impressed, possibly digitate.

		length	width (mm.)
Holotype.	Internal mould of brachial valve (BB.28997)	6·0	—
Paratypes.	Internal mould of brachial valve (BB.29002)	8·5	10·5
	Internal and external moulds of pedicle valve (BB.28998–99)	9·0	—
	Internal and external moulds of pedicle valve (BB.29000–01)	6·5	8·0

Horizons and localities. Gelli-grîn Group : BB.28998–99, BB.29002 from calcareous ashes cropping out 400 ft. east-south-east of Bryn-briglas Farm ; BB.28997 from calcareous ashes exposed on Creigiau Bychain, 600 yds. north-east of Glyn-bach ; BB.29000–01 from calcareous ashes exposed at Myrddin Marad.

Discussion. Rare moulds, referable to the genus *Orthambonites*, have been collected from rocks of the Gelli-grîn Group but are sufficiently distinctive to be described as a new species. The shell outline is subquadrate for although young shells tend to be widest along the hinge-line, lateral increment was accelerated during later stages of growth, and for four adult brachial valves the mean percentage length relative to maximum width, which was anterior of the hinge-line, was 70% (variance 90·7). Both valves were strongly and evenly convex in longitudinal profile due partly to the development of long interareas : the mean percentage thicknesses relative to lengths of three pedicle and three brachial valves were 32·3 (ranging between 30–34) and 24 (range 23–25) respectively. Despite the strong convexity of the brachial valve, the dorsal sulcus was vestigial amounting to no more than a slight median flattening involving the two submedian costae, and only discernible in transverse profile. The ornamentation consisted of 13, 14, 15 and 16 costae in 1, 0, 2 and 1 external ventral moulds, with an average wavelength of 0·57 mm. (range 0·5–0·7 mm.) 5 mm. antero-medianly of the umbones of three pedicle valves.

The subtriangular ventral muscle field, which was deeply impressed on the floor of the pedicle valve, was about as long as wide in young valves, but during adult growth the anterior border expanded very much faster so that the mean percentage length relative to the length of four internal moulds was 30 (variance 11·67). The dorsal adductor muscle field was also well defined and its mean percentage length

relative to the length of four internal moulds was 58 (variance 12·67). But the cardinalia constituted the most distinctive features of the dorsal interior for the cardinal process was strongly developed even in young valves, almost filling the notothyrium as a thick, ventrally swollen shaft, and the brachiophores long and blade-like with an average percentage extension relative to the length of three internal moulds of 23 (range 18–27).

Apart from the high interareas which are not common attributes of described species of *Orthambonites* the two most distinctive features are the lack of a definite sulcus in a brachial valve that is so strongly convex and the long blade-like brachiophores reminiscent of those typical of *Hesperorthis*. A few known paucicostate species like *O. mostellerensis* Cooper and *O. rotundiformis* Cooper (1956 : 306, 311) are also feebly sulcate and the multicostate *O. brachiophorus* Cooper (1956 : 298) is equipped with similar brachiophores ; but in no other species are both these features found in combination.

Davidson (1869, pl. 35, figs. 1–3) figured three shells as *Orthis calligramma* Dalman which are more appropriately relegated to the genus *Orthambonites* as at present defined, and are purported to come from " Moelydd, near Bala ". These specimens together with others labelled as having been collected from the same locality are now preserved in the British Museum (BB.13455, BB.28840–48). They are all complete, undeformed shells or valves which could not have come from the Bala district ; some at least, judging from the adherent matrix as well as the external morphology of the shells, were almost certainly taken from the mudstones associated with the Craighead Limestones and are representatives of *Orthambonites playfairi* Reed (see Williams 1962 : 97).

Subfamily PRODUCTORTHINAE Schuchert & Cooper 1931

Genus *NICOLELLA* Reed 1917

Type species. *Orthis actoniae* J. de C. Sowerby by original designation of Reed (1917 : 860).

Nicolella actoniae (J. de C. Sowerby)

(Pl. 1, figs. 15–19 ; Text-fig. 6)

1839 *Orthis actoniae* J. de C. Sowerby : 639, pl. 20, fig. 16r, *non* fig. 16e.

Diagnosis (emended). Large, plano- to slightly concavo-convex, subquadrate to mucronate *Nicolella* with evenly convex pedicle valve less than one-third as deep as long and short, curved, orthocline ventral interarea ; brachial valve commonly widest at hinge-line, almost two-thirds as long as wide with very short, curved anacline interarea ; ornamentation consisting of 11 to 15 angular costae, wavelength about 1 mm. at 5 mm. anterior of dorsal umbo, costellae not typically developed within 7·5 mm. of dorsal umbo but with 3ā usually arising earlier than 1ā, concentric lamellose outgrowths strong but irregularly disposed ; teeth strong, commonly striated, supported by short, receding dental lamellae, ventral muscle

field elongately oval in outline extending anterior of umbo for about two-fifths the length of valve, submedian lobes not enclosing lanceolate adductor impressions anteriorly ; ventral pallial sinus pattern saccate, *vascula media* closely adjacent posteriorly splayed and divided anteriorly ; cardinal process ridge-like and erect, flanked by chilidial plates, brachiophores short, widely splayed and together with notothyrial platform commonly heavily encased in secondary shell and united to short median ridge, dorsal adductor field small, obscured by proximal ends of *vascula myaria* and *media*, pallial sinus pattern saccate modified to digitate.

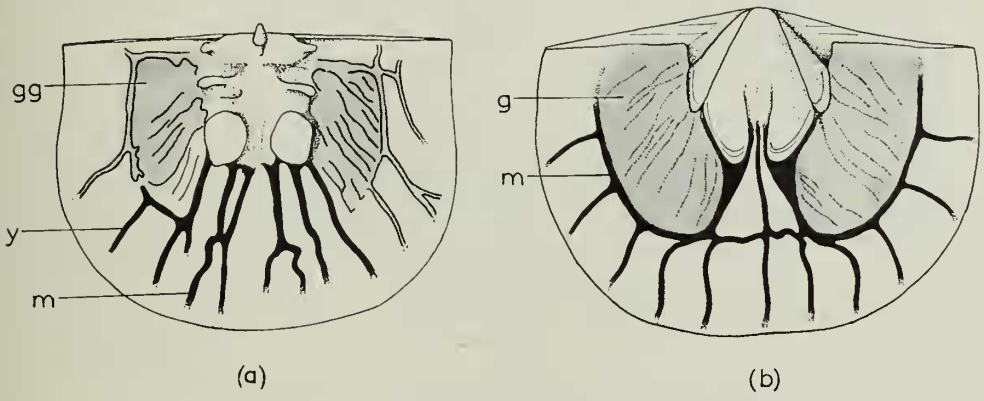

FIG. 6. The dorsal (a) and ventral (b) interiors of *Nicolella actoniae* (J. de C. Sowerby), ×2·5 approx., showing the pallial sinus patterns : *g*, impression of gonocoele ; *gg*, *vascula genitalia* ; *m*, *vascula media* ; *y*, *vascula myaria*.

		length	width (mm.)
LECTOTYPE.	Internal mould of pedicle valve (G.S.M. Geol. Soc. Coll. 6883)	19·0	23·0
OTHER MATERIAL.	Internal mould of pedicle valve (B.74772)	17·8	29·5
	External mould of brachial valve (BB.27315)	18·3	24·8
	Internal mould of brachial valve (BB.27317)	—	—
	Internal mould of brachial valve (BB.28959)	16·0	21·0

HORIZON AND LOCALITIES. Actonian Stage : the lectotype, G.S.M. 6883 and B.74772 from buff-weathering sandstones, "Acton Scott", Shropshire ; BB.27315 and 27317 from buff-weathering sandstones exposed in a stream section by the east side of a road-bridge about 1,000 ft. west-south-west of Hatton, Shropshire ; BB.28959 from loose blocks near Acton Scott Church, possibly from the quarry of Castle Hill, one-third of a mile west-south-west of Acton Scott.

Nicolella actoniae J. de C. Sowerby *obesa* subsp. nov.
(Pl. 2, figs. 1–5, 7)

Diagnosis. Plano- to slightly concavo-convex, mucronate *Nicolella* with highly convex pedicle valve over two-fifths as deep as long and short, curved, orthocline ventral interarea ; brachial valve widest at hinge-line, about three-fifths as long as wide, with short, curved, anacline interarea ; radial ornamentation interrupted by strong, irregularly developed, concentric lamellose outgrowths and consisting of 11 to 14 angular costae with wavelength of about 1 mm. at 5 mm. anterior of dorsal umbo, costellae fairly common within 7·5 mm. of dorsal umbo and with 3ā usually originating before 1ā ; teeth, commonly striated, supported by short, receding dental lamellae, ventral muscle field oval and extending anterior of umbo for about two-fifths the length of valve, submedian diductor lobes not enclosing lanceolate adductor impressions anteriorly ; ventral pallial sinus pattern saccate to lemniscate with closely situated *vascula media* dividing anteriorly ; cardinal process, erect and ridge-like flanked by chilidial plates ; brachiophores, short, widely divergent, extending on either side of median plane for about one-third of the length of hinge-line, and commonly ankylosed to short median ridge, by heavy deposits of secondary shell ; dorsal adductor field poorly impressed extending anteriorly for about one-third the length of brachial valve ; dorsal pallial sinus pattern digitate.

		length	width (mm.)
Holotype.	Internal mould of pedicle valve (BB.29003)	12·5	—
Paratypes.	Internal mould of pedicle valve (BB.29004)	15·5	—
	External mould of brachial valve (BB.29005)	9·5	16·5
	Internal mould of brachial valve (BB.29006)	12·5	—
	External mould of brachial valve (BB.29007)	11·0	16·5

Horizon and localities. Gelli-grîn Group: Holotype, BB.29003 from calcareous ashes above the limestone in the old quarries and BB.29005–07 from calcareous ash crags 75 ft. south-east of deserted buildings in Ffridd Bach, south of Maesmeillion ; BB.29004 from ashy mudstones exposed on the right bank of the Hirnant, 1,200 ft. east-north-east of Ty'n-y-wern.

Discussion. Representatives of the genus *Nicolella* are known to occur sporadically throughout the Upper Ordovician rocks of Britain and are probably remnants of a number of independent stocks although at present it is customary to identify them all as being closely related to *N. actoniae* (J. de C. Sowerby 1839) the type species for the genus. This procedure is, to some extent, understandable in that Sowerby's brief diagnosis was based on two distinct orthaceid moulds (see Williams 1955 : 406) and no emended description has ever been published. A small

collection of moulds from Actonian sandstones exposed in the vicinity of Acton Scott, which are topotypic with the lectotype chosen by Williams (1955 : 406), has been used to provide a revised account of the species and it is clear that specimens of *Nicolella* found in the Gelli-grîn beds of the Bala district belong to a closely related group meriting only sub-specific recognition.

TABLE 2

	A		B	
$\bar{l}$ mm. (var. l)	5·4	(8·668)	12·5	(38·062)
$\bar{w}$ mm. (var. w)	9·0	(18·548)	18·7	(64·986)
r	0·989		0·978	
[1]$\log_e \bar{l}$ (var. $\log_e$ l)	1·563	(0·2578)	2·4185	(0·2175)
$\log_e \bar{w}$ (var. $\log_e$ w)	2·0952	(0·2061)	2·84	(0·1716)
r_e	0·989		0·968	
α (var. α)	0·8942	(0·00031)	0·8883	(0·00207)

TABLE 2. Statistics of length (l) and maximum width (w) of 59 brachial valves of *Nicolella actoniae obesa* subsp. nov. (A) and of 26 brachial valves of *Nicolella actoniae* (J. de C. Sowerby) (B).

TABLE 3

	A		B	
$\bar{l}$ mm. (var. l)	8·95	(11·804)	15·1	(20·912)
$\bar{th}$ mm. (var. th)	3·7	(2·566)	4·6	(1·928)
r	0·843		0·988	
a (var. a)	0·4662	(0·00483)	0·3036	(0·00011)

TABLE 3. Statistics of length (l) and maximum depth (th) of 15 pedicle valves of *Nicolella actoniae obesa* subsp. nov. (A) and of 22 pedicle valves of *Nicolella actoniae* (J. de C. Sowerby) (B).

TABLE 4

$\bar{l}$ mm. (var. l)	16·4	(13·524)
$\bar{sc}$ mm. (var. sc)	6·8	(3·694)
r	0·981	
a (var. a)	0·5226	(0·00103)

TABLE 4. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for 12 specimens of *Nicolella actoniae* (J. de C. Sowerby).

TABLE 5

	A		B	
$\bar{l}$ mm. (var. l)	4·9	(1·231)	7·3	(1·335)
$\bar{w}$ mm. (var. w)	4·4	(0·686)	6·6	(0·967)
r	0·785		0·956	
a (var. a)	0·7465	(0·3315)	0·8511	(0·00623)

TABLE 5. Statistics of length (l) and maximum width (w) of ventral muscle scars of eight pedicle valves of *Nicolella actoniae obesa* subsp. nov. (A) and of twelve pedicle valves of *Nicolella actoniae* (J. de C. Sowerby) (B).

[1] $\log_e \bar{l}$ (and all similarly styled terms) is an approximation to $\overline{\log_e} \bar{l}$ derived in the manner suggested by Kermack & Haldane (1950)—see Williams 1962 : 72.

In outline and profile the Bala and Acton Scott samples are very much alike. Both tend to be widest at the hinge-line and commonly attain a mucronate condition and although the Acton Scott moulds are relatively longer, comparisons of their growth rates and indices of inherent shape (Table 2) show that this difference is not important. The pedicle valves of both samples were evenly convex in lateral and longitudinal profiles but those from Bala were consistently deeper relative to length and a comparison of growth rates (Table 3) shows that their depth increased at a significantly faster rate than those from Acton Scott ($p < \cdot 02$).

Shells from both lots were ornamented by sporadically occurring concentric lamellae and also by strong, angular costae with a mean wavelength (with variance) 5 mm. antero-medianly of the dorsal umbones, of 1·05 mm. (0·023) and 1·03 (0·079) in 15 and 27 brachial valves of *N. actoniae* and the new subspecies respectively. The basic pattern in both samples consisted of 5 costae on either side of the median plane to the brachial valve with primary 1 apparently arising very early from primary 2 just anterior of the protegulum which was about 0·3 mm. long. These 10 costae occupied a sector of approximately 120° about the median line and during subsequent growth of the shell new costae arose within the wide postero-lateral sectors. Thus at the 7·5 mm. growth stage 11, 12, 13, 14 and 15 primaries were counted in 1, 1, 3, 2 and 2 brachial valves of *N. actoniae* compared with 6, 11, 9, 7 and 0 brachial valves of *N. actoniae obesa*. Within this growth stage, too, 3 out of 10 brachial valves belonging to the Acton Scott sample had developed secondary costellae branching internally from one or more of the 10 primary costae with secondary 3ā arising before 1ā in two out of three specimens in the former sample and in eight out of fourteen specimens in the latter. The Bala shells therefore tend to have fewer costae but more costellae in early stages of growth but the differences are not important.

The few data available for a comparison of internal morphology show that in this respect too, the samples are similar. The suboval ventral muscle fields in three pedicle valves of the new subspecies were, on an average, two-fifths as long as the valves and are indistinguishable in relative length from those of *N. actoniae* (Table 4) ; while comparisons of the growth rates and indices of inherent shape for their outlines (Table 5) show no important difference. It is, however, noteworthy that Bala shells attaining a dorsal length of about 12 mm. were excessively thick due to heavy secretion of secondary shell substance so that the intersetal eminences (see Williams & Wright 1963 : 19) stood high above the internal margins of the valves. A comparable condition was found in the Acton Scott sample only in shells in excess of 18 mm. long which suggests that such adults grew faster and attained an absolutely greater size.

In review then it can be said that the two samples are closely related morphologically. None the less the Bala shells were significantly deeper in their ventral profiles and were also probably smaller in absolute size and in recognition of these differences the new subspecies is proposed.

Family DOLERORTHIDAE Öpik 1934

Genus ***DOLERORTHIS*** Schuchert & Cooper 1931

TYPE SPECIES. *Orthis interplicata* Foerste by original designation of Schuchert & Cooper (1931 : 88).

Dolerorthis duftonensis (Reed) ***prolixa*** subsp. nov.

(Pl. 2, figs. 6, 8–13)

DIAGNOSIS. Subquadrate unequally biconvex *Dolerorthis* with rectangular or slightly obtuse cardinal angles, brachial valve about three-quarters as long as wide, gently sulcate medianly but evenly convex in longitudinal and lateral profiles, less than one-fifth as deep as long, dorsal interarea anacline, strongly developed, about one-eighth as long as valve, notothyrium open ; pedicle valve highly convex over one-quarter as deep as long, triangular in longitudinal profile with long apsacline interarea, delthyrium open but very narrow to slit-like ; ornamentation finely costellate, cancellated by fine concentric lamellae at about 7 per mm. 5 mm. anterior of dorsal umbo, with 2 costellae per mm. at about 10 mm. antero-medianly of dorsal umbo, costellae evenly rounded in transverse profile with parallel sides, arising by lateral branching from 10 to 14 primaries and including internal secondaries originating almost invariably within 5 mm. of dorsal umbo in second, third, fourth and fifth sectors so that 3ā was commonly earliest and 2ā the latest ; teeth strong, dental lamellae slightly divergent, strong extending anteriorly of umbo above floor of valve for about one-fifth the length of valve, muscle scar extending anteriorly for about one-third the length of pedicle valve, initially cordate in outline and about as wide as long but later extended anteriorly to become subrhomboidal, although lanceolate median adductor scar never completely surrounded by diductor submedian lobes ; ventral pallial sinus pattern saccate with contiguous *vascula media* ; cardinal process simple, blade-like, sporadically flanked in adult brachial valves by pair of low ridges on notothyrial floor, brachiophores simple, rod-like with their bases extending anteriorly of dorsal umbo for less than one-fifth the length of valve and about one-half as long as wide, dorsal adductor muscle field quadripartite extending anteriorly of umbo for over one-half the length of brachial valve, posterior scars larger than anterior, median ridge low, dorsal pallial sinus pattern apocapate.

		length	width (mm.)
HOLOTYPE.	Internal and external moulds of brachial valve (BB.29008–09)	12·0	14·0
PARATYPES.	Internal mould of brachial valve (BB.29010)	19·5	23·0
	Internal mould of pedicle valve (BB.29011)	16·0	17·5
	External mould of pedicle valve (BB.29012)	—	—
	External mould of brachial valve (BB.29013)	—	21·5
	Internal mould of pedicle valve (BB.29014)	27·0	29·0

Horizon and localities. Gelli-grîn Group : BB.29008–09 from calcareous ashes exposed on the northern flank of the southernmost outlier of Rhiwlas rocks on Creigiau Bychain about 500 yds. north-east of Glyn-bach ; BB.29011 and 29013 from calcareous ashes above limestone exposed in quarries east of fence and 650 ft. west-north-west of BM.1407.6, south side of Bryn-Pig ; BB.29010 and 29014 from calcareous ashes above limestone in old quarry, 1,100 ft. west-south-west of Gelli-grîn Farm ; BB.29012 from ashy mudstones forming crags 1,600 ft. south-south-east of Bryn-bedwog Farm.

Discussion. *Dolerorthis* is fairly common in the Gelli-grîn Group and sufficiently good collections were made to provide data for a number of attributes (see Tables 6 to 15). The stock is clearly related to *Dolerorthis duftonensis* (Reed 1910 : 295) but a comparative study of a small sample of topotypic *D. duftonensis* from Upper Longvillian mudstones exposed on the Alston Road, north-east of Melmerby (Loc. H of Dean 1959 : 210) shows that the north Welsh shells were different enough to warrant taxonomic recognition.

In the brachial valves despite an overall likeness, three distinct differences can be demonstrated. The Welsh *Dolerorthis*, are, on an average, three-quarters as long as wide, a proportion that did not greatly change during growth (Table 6). Five brachial valves of *D. duftonensis*, varying in length from 9·4 to 23·5 mm. had a mean percentage length relative to width of 82·3 (variance 45·128) and a Rank Sum test shows that they are significantly longer ($p < ·05$). The average percentage depth relative to length of seven brachial valves of *D. duftonensis* was 17·3 (variance 13·015), very like that for the new subspecies (Table 7) as were also the relative length of the dorsal adductor scars (Table 11) and the relative extension of the brachiophore bases anterior of the dorsal umbo (Table 9). But comparisons of relative growth rates governing the anterior extension of the dorsal interareas (Table 8) and the lateral extension of the brachiophore bases (Table 10) show that they had been significantly faster ($p < ·001$ and $p < ·05$ respectively) in the new subspecies.

A few differences have also been observed in the morphology of the pedicle valve. Three valves of *D. duftonensis* 12, 11 and 13·5 mm. long, had a relative percentage thickness of 37·5, 50·0 and 44·4 compared with an average of only 29 for the Welsh valves (Table 12). In both stocks the ventral muscle field tend to be cordate and about as long as wide during early growth stages. The anterior extension of the entire scar was, however, greatly and comparably accelerated relative to its width in adult valves (Table 15), but not relative to the length of the valves. Thus in five pedicle valves, ranging in length from 10·5 to 17·0 mm., the mean percentage length of scars relative to valves was 26·6 (variance 3·61) ; a Rank Sum test showed that these relative lengths were significantly less ($p = ·028$) than those for the new subspecies (Table 14). The anterior extension of the dental lamellae relative to the valve length is also less in *D. duftonensis* with a mean percentage (and variance) of 17·7 (2·49) in five valves, but the difference was not important.

The radial ornamentation of this group of *Dolerorthis* is quite distinctive. In the new subspecies, costellae arose by lateral branching from 10, 11, 12, 13 and 14

primary costae in 2, 8, 3, 2 and 1 brachial valves respectively and were sufficiently fine to number 1 and 2 per mm. in 1 and 7 brachial valves respectively at 10 mm. anterior of the umbones. Secondary internal branching took place quite early during growth. Thus within 5 mm. of the umbones of 20 brachial valves, 1ā, 2ā, 3ā, 4ā, 5ā and 6ā occurred in 10, 19, 20, 19 and 15 valves respectively. In contrast external branching within the same growth stages of the same valves was rare for 2a°, 3a°, 4a° and 5a° appeared in only 2, 4, 5 and 4 valves respectively. The relative occurrence of the internal costellae may be summarised in the following manner : 3ā appears before 4ā in 14 out of 20 valves, 4ā before 5ā in 15 out of 20 valves (in two valves they arose at about the same growth stage) and 5ā before 2ā in 15 out of 20 valves. These patterns are consistent with those observed on a few brachial valves of *D. duftonensis*.

In summary then, *D. duftonensis prolixa* differs from *D. duftonensis*, in its relatively longer brachial valve and dorsal interarea, in the lateral spread of its brachiophores, in its shallower pedicle valve and in its relatively longer ventral muscle field. Both stocks also bear some resemblance to *D. tenuicosta* (Williams 1955 : 406) but can immediately be distinguished, amongst other features, by the relative coarseness of their radial ornamentation.

TABLE 6

$\bar{l}$ mm. (var. l)	11·2	(29·189)
$\bar{w}$ mm. (var. w)	14·9	(45·799)
r	0·981	
a (var. a)	1·253	(0·00281)

TABLE 6. Statistics of length (l) and maximum width (w) of 23 brachial valves of *Dolerorthis duftonensis prolixa* subsp. nov.

TABLE 7

$\bar{l}$ mm. (var. l)	11·5	(22·836)
$\bar{th}$ mm. (var. th)	2·0	(1·221)
r	0·718	
$\log_e \bar{l}$ (var. $\log_e$ l)	2·3613	(0·1605)
$\log_e \bar{th}$ (var. $\log_e$ th)	0·5349	(0·2759)
r_e	0·742	
α (var. α)	1·311	(0·02665)

TABLE 7. Statistics of length (l) and thickness (th) of 31 brachial valves of *Dolerorthis duftonensis prolixa* subsp. nov.

TABLE 8

	A		B	
$\bar{l}$ mm. (var. l)	13·4	(18·328)	12·4	(39·32)
$\bar{in}$ mm. (var. in)	1·6	(0·343)	1·3	(0·32)
r	0·858		0·972	
$\log_e \bar{l}$ (var. $\log_e$ l)	2·5498	(0·0970)	2·4037	(0·2279)
$\log_e \bar{in}$ (var. $\log_e$ in)	0·4208	(0·1231)	0·1391	(0·1839)
r_e	0·867		0·983	
a (var. a)	0·137	(0·00013)	0·092	(0·00005)

TABLE 8. Statistics of length of brachial valve (l) and length of dorsal interarea (in) for 41 specimens of *Dolerorthis duftonensis prolixa* subsp. nov. (A) and for 11 specimens of *D. duftonensis* (Reed) (B).

TABLE 9

	A		B	
$\bar{l}$ mm. (var. l)	13·1	(17·96)	12·4	(39·32)
$\bar{c}$ mm. (var. c)	2·4	(0·505)	2·1	(1·204)
r	0·932		0·97	
α (var. α)	0·1677	(0·00011)	0·1749	(0·0002)

TABLE 9. Statistics of length of brachial valve (l) and length of cardinalia bases (c) for 39 specimens of *Dolerorthis duftonensis prolixa* subsp. nov. (A) and for 11 specimens of *D. duftonensis* (B).

TABLE 10

	A		B	
$\bar{l}$ mm. (var. l)	2·4	(0·586)	2·1	(1·204)
$\bar{w}$ mm. (var. w)	4·9	(1·912)	3·5	(2·563)
r	0·884		0·972	
a (var. a)	1·807	(0·02161)	1·459	(0·0134)

TABLE 10. Statistics of length (l) and maximum width (w) of the cardinalia bases for 35 brachial valves of *Dolerorthis duftonensis prolixa* subsp. nov. (A) and for 11 brachial valves of *D. duftonensis* (Reed) (B).

TABLE 11

	A		B	
$\bar{l}$ mm. (var. l)	14·4	(21·295)	13·4	(38·79)
$\bar{sc}$ mm. (var. sc)	7·9	(4·729)	7·0	(9·8)
r	0·966		0·987	
$\log_e \bar{l}$ (var. $\log_e$ l)	2·6208	(0·097)	2·4995	(0·1946)
$\log_e \bar{sc}$ (var. $\log_e$ sc)	2·0246	(0·0744)	1·8579	(0·1818)
r_e	0·985		0·99	
α (var. α)	0·8758	(0·00176)	0·9665	(0·00232)

TABLE 11. Statistics of length of brachial valve (l) and extension of adductor scars anterior of the umbo (sc) of 15 specimens of *Dolerorthis duftonensis prolixa* subsp. nov. (A) and of 10 specimens of *D. duftonensis* (Reed) (B).

TABLE 12

$\bar{l}$ mm. (var. l)	14·7	(18·221)
$\bar{th}$ mm. (var. th)	4·2	(1·81)
r	0·67	
a (var. a)	0·3152	(0·00209)

TABLE 12. Statistics of length (l) and maximum depth (th) of 29 pedicle valves of *Dolerorthis duftonensis prolixa* subsp. nov.

TABLE 13

$\bar{l}$ mm. (var. l)	17·9	(24·924)
$\bar{dl}$ mm. (var. dl)	3·7	(1·739)
r	0·761	
a (var. a)	0·2642	(0·00244)

TABLE 13. Statistics of length of pedicle valve (l) and anterior extension of dental lamellae (dl) of 14 specimens of *Dolerorthis duftonensis prolixa* subsp. nov.

TABLE 14

$\bar{l}$ mm. (var. l)	14·8	(14·14)
$\bar{sc}$ mm. (var. sc)	5·0	(2·835)
r	0·762	
$\log_e \bar{l}$ (var. $\log_e$ l)	2·6651	(0·0631)
$\log_e \bar{sc}$ (var. $\log_e$ sc)	1·5514	(0·1079)
r_e	0·765	
α (var. α)	1·308	(0·01867)

TABLE 14. Statistics of length of pedicle valve (l) and length of ventral muscle field (sc) of 40 specimens of *Dolerorthis duftonensis prolixa* subsp. nov.

TABLE 15

$\bar{l}$ mm. (var. l)	5·0	(2·607)
$\bar{w}$ mm. (var. w)	4·0	(1·067)
r	0·896	
$\log_e \bar{l}$ (var. $\log_e$ l)	1·5615	(0·0997)
$\log_e \bar{w}$ (var. $\log_e$ w)	1·3402	(0·0669)
r_e	0·9342	
α (var. α)	0·8191	(0·00329)

TABLE 15. Statistics of length (l) and maximum width (w) of the ventral muscle field of 28 specimens of *Dolerorthis duftonensis prolixa* subsp. nov.

Dolerorthis sp.

(Pl. 2, figs. 14–16 ; Text-fig. 7)

MATERIAL (Figured).	length	width (mm.)
Internal mould of pedicle valve (BB.29152)	11·5	12·5
Incomplete internal mould of brachial valve (BB.29153)	7·0	—
Fragment of external mould of brachial (?) valve (BB.29154)	—	—

Horizon and locality. Allt Ddu Group : all specimens from sandstone and siltstone exposures about 80 ft. north of the gutter on Craig y Gath (type locality of *Howellites ultima* Bancroft 1945 : 209).

Discussion. *Dolerorthis duftonensis* (Reed) *prolixa* subsp. nov. first occurs just above the Pont-y-Ceunant Ash and is common throughout the succeeding ashes and limestones of the Gelli-grîn Group. A few specimens belonging to the genus have also been recovered from one exposure of the highest Allt Ddu sandstones and siltstones and at first sight appear to be quite distinct from the new subspecies. In terms of shape and outline the differences are not important for the faintly sulcate brachial valve is slightly less than four-fifths as long as wide and over one-quarter as deep as long compared with a relative depth of about one-third for the pedicle valve. A fragment of what is probably the external mould of a brachial valve shows that the radial ornamentation was probably costate but the entire mould could not have been more than 8 mm. long and this condition could have been related to the small size of the valve. The moulds, however, are not the remains of young shells because the pallial sinus patterns are beautifully preserved for both valves. These impressions are usually found in only mature adult or gerontic specimens and they are not seen in the interiors of *D. duftonensis prolixa* until the shells are about twice the size of those from the Allt Ddu beds. In other words the specimens being described grew at about one-half the rate of their younger relatives but whether this difference reflects a genetic change or simply an unfavourable environment prior to the deposition of the calcareous ashes, when many of the Gelli-grîn brachiopod species tended to be larger than average, remains to be seen.

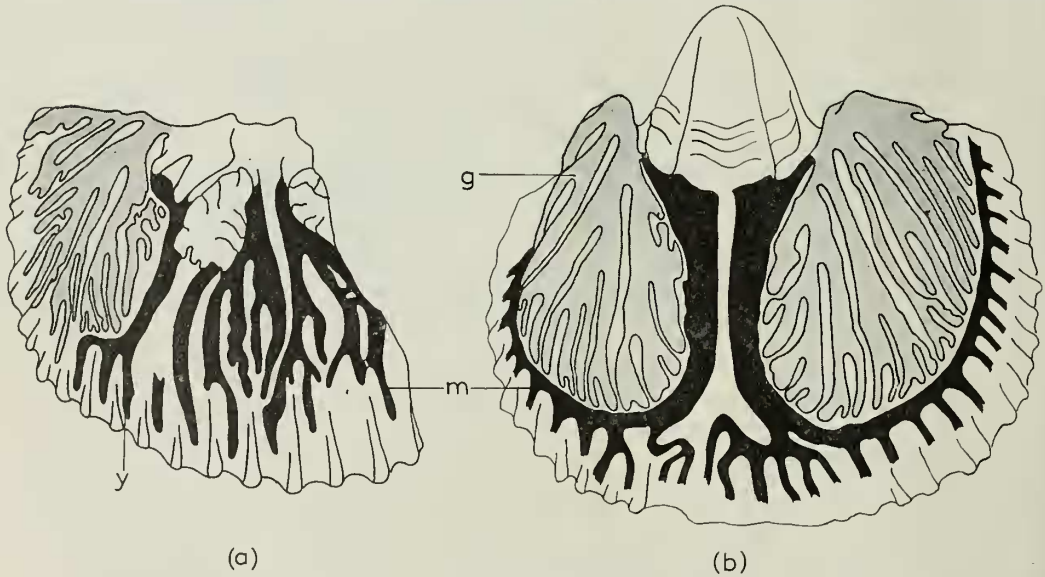

Fig. 7. The dorsal (a) and ventral (b) internal moulds of *Dolerorthis* sp., ×6·0 approx., showing the pallial sinus patterns : *g*, impression of gonocoele ; *m*, *vascula media* ; *y*, *vascula myaria*.

The most interesting aspect of the pallial sinus impressions (Text-fig. 7) is the abbreviation of the posterolateral arcs of the *vascula media* in the pedicle valve and the existence of *vascula myaria* in the brachial valve. These features suggest that the ventral saccate condition and the dorsal apocopate pattern of later *Dolerorthis* (Öpik 1934 : 56 ; Williams 1956 : 278) were secondarily derived.

Family DINORTHIDAE Schuchert & Cooper 1931

Genus ***DINORTHIS*** Hall & Clarke 1892

Type species. *Orthis pectinella* Emmons by original designation of Hall & Clarke (1892 : 195).

Dinorthis flabellulum (J. de C. Sowerby)
(Pl. 3, figs. 1–4)

1839 *Orthis flabellulum* J. de C. Sowerby : 639, pl. 21, fig. 8, *non* pl. 19, fig. 8.

Diagnosis (emended). Subquadrate, convexo-plane to gently concave *Dinorthis* with evenly convex brachial valve almost one-quarter as deep as long and pedicle valve, less than three-quarters as long as wide, essentially planar in profile but with raised umbo and margins commonly gently deflected ventrally to give gently concave disposition ; ventral interarea apsacline, dorsal interarea commonly orthocline, up to one-tenth as long as brachial valve ; radial ornamentation consisting of strong costae with wavelength of almost 0·8 mm., 5 mm. antero-medianly of ventral umbo, and commonly numbering 24 to 26 in pedicle valves over 10 mm. long ; ventral muscle scar elongately subrectangular, extending anteriorly for almost one-half the length of pedicle valve and about four-fifths as wide as long, teeth small, dental lamellae divergent, short, less than one-tenth as long as pedicle valve ; cardinal process fully differentiated into shaft and expanded, crenulated myophore in about one-half of brachial valves between 12 and 20 mm. long, brachiophores simple and unsupported, suboval in section and extending forward of dorsal umbo at their junction with valve floor for about one-sixth the length of brachial valve, and for less than two-thirds the lateral extension of simple sockets ; dorsal adductor field, suboval and extending anterior of dorsal umbo for over one-half the length of brachial valve but rarely impressed on either side of short, low median ridge.

Material (Figured).	length	width (mm.)
Internal mould of pedicle valve (BB.28934)	24·1	26·8
Internal mould of brachial valve (BB.29023)	20·0	27·9
External mould of pedicle valve (BB.28935)	19·2	28·3
External mould of brachial valve (BB.29024)	20·8	27·5

Horizon and locality. Costonian Stage : all specimens from yellow weathering sandstones exposed in the vicinity of Coston Farm, one mile east-south-east of Clunbury.

Dinorthis berwynensis (Whittington)
(Pl. 3, figs. 5, 6, 9, 10)

1938 *Orthis calligramma* var *berwynensis* Whittington : 243, pl. 10, figs. 1–3.

Diagnosis (emended). Subquadrate, convexo-plane to gently concave *Dinorthis* with brachial valve over one-quarter as deep as long, tending to be more strongly convex medianly and pedicle valve, less than three-quarters as long as wide, essentially planar in transverse profile but with raised umbo, and shallow sulcus, originating at about 6 mm. anterior of umbo and embracing about 6 costae, together imparting slight concavity to longitudinal profile ; ventral interarea apsacline, dorsal interarea commonly orthocline about one-twelfth as long as brachial valve ; radial ornamentation in pedicle valves over 5 mm. long, costate and consisting of 21 to 26 costae with wavelength of nearly 0·5 mm., 5 mm. antero-medianly of ventral umbo ; teeth small, dental lamellae, divergent, short, about one-seventh the length of pedicle valve, subrectangular ventral muscle scar over nine-tenths as wide as long and extending anterior of ventral umbo for less than two-fifths the length of pedicle valve ; cardinal process commonly fully differentiated into shaft and expanded, crenulated myophore in brachial valves over 8·0 mm. long, brachiophores simple and unsupported, suboval in cross section and extending forward of dorsal umbo at their junction with valve floor for over one-sixth the length of brachial valve and for over one-half lateral extension of simple sockets, dorsal adductor field suboval and extending forward of umbo for about one-half the length of brachial valve but rarely impressed on either side of short, low median ridge.

Material (Figured).	length	width (mm.)
Internal mould of pedicle valve (BB.28982)	6·3	8·4
Internal mould of brachial valve (BB.28983)	—	—
External mould of pedicle valve (BB.28984)	11·9	—
Internal mould of brachial valve (BB.29025)	3·8	—

Horizons and localities. Glyn Gower Group : BB.28982 from siltstones exposed between parallel paths on the west side of Y Foel, 1,300 ft. south-south-east of Coed-y-foel-uchaf Farm ; BB.28983–84 from siltstone crags in wood immediately east of Cefn-bodig Farm. Lower Allt Ddu Group : BB.29025 from siltstones immediately above the Fron-dderw Ash and about 600 ft. north of Fron-dderw Farm.

Dinorthis berwynensis (Whittington) *angusta* subsp. nov.
(Pl. 3, figs. 7, 8, 11–14)

Diagnosis. Subquadrate, convexo-plane to gently concave *Dinorthis* with brachial valve nearly two-fifths as deep as long, tending to be more strongly convex medianly and pedicle valve less than four-fifths as long as wide, essentially planar

in transverse profile but with raised umbo and shallow sulcus, originating at about 6 mm. anterior of umbo and embracing 7 or 8 costae, together imparting a slight concavity to the longitudinal profile ; ventral interarea apsacline, dorsal interarea commonly orthocline, about one-twelfth as long as brachial valve ; radial ornamentation costate and, in pedicle valves over 5 mm. long, consisting of 21 to 26 costae with wavelength of over 0·4 mm., 5 mm. antero-medianly of ventral umbo ; teeth small, dental lamellae divergent, short, about one-sixth as long as pedicle valve, subrectangular ventral muscle scar less than nine-tenths as wide as long and extending forward of umbo for less than two-fifths the length of pedicle valve ; cardinal process fully differentiated into shaft and expanded, crenulated myophore in valves more than 6 mm. long, brachiophores simple and unsupported, suboval in cross section and extending forward of dorsal umbo at their junction with valve floor for over one-fifth the length of brachial valve and for over one-half the lateral extension of simple sockets, dorsal adductor field suboval and extending forward of umbo for about one-half the length of brachial valve but rarely impressed on either side of short, low median ridge.

		length	width (mm.)
Holotype.	Internal and external moulds of pedicle valves (BB.28978–79)	14·3	19·6
Paratypes.	Internal and external moulds of pedicle valve (BB.28980–81)	11·0	—
	Internal mould of brachial valve (BB.29026)	6·7	7·1
	Internal mould of brachial valve (BB.29027)	12·0	—

Horizon and locality. Allt Ddu Group : all specimens from fine sandstones and mudstones immediately below the Pont-y-Ceunant Ash and exposed in crags north of the drive to Y Garnedd.

Discussion. *Dinorthis* is known to occur in the upper part of the Glyn Gower Group as well as in the Allt Ddu Group, but examples are common only in the strata succeeding the Fron-dderw Ash, where they are associated with *Heterorthis retrorsistria*, and again in the sandy beds immediately underlying the Gelli-grîn Group. The radial ornamentation of the specimens recovered is almost invariably costate which immediately separates them from the Costonian and Soudleyan species of *Plaesiomys* described by Bancroft (1945 : 240–245) and suggests affinities with the similarly ornamented *Dinorthis flabellulum* (J. de C. Sowerby) and *D. berwynensis* (Whittington). The older stock is indistinguishable in every aspect of its morphology from the latter species, and a sample taken from siltstones just below and above the Fron-dderw Ash has been used to provide an emended diagnosis of *D. berwynensis*. The high Allt Ddu forms differed significantly from both species but is much more removed from *D. flabellulum* and, in order to recognise this disparity, it has been described as a new subspecies *D. berwynensis angusta*.

The sample of *D. flabellulum* was not entirely satisfactory in that it consisted mainly of mature shells, commonly up to three times as large as those in the collections from Bala, and this is probably reflected in the number of costae ornamenting the pedicle valves (Table 22). The differences are not important, but, as can be seen, larger shells tend to have more costae which arose in the postero-lateral areas well away from the umbo, so that the higher modal value for *D. flabellulum* is to be expected. This would also explain the apparent anomaly of the broader costae of *D. flabellulum*. At a distance of 5 mm. antero-medianly of the ventral umbo the mean wavelength (with variance) of the costae of 23 specimens of *D. flabellulum* was 0·77 (0·033) compared with 0·48 (0·003) for 16 specimens of *D. berwynensis* and 0·44 (0·006) for 17 specimens of the new subspecies. In all three samples, the costae are smoothly rounded in transverse profile but those of *D. flabellulum* are significantly wider ($p < ·001$) than those ornamenting the Bala specimens. With respect to the influence of size on the pattern of ornamentation, one other fact is noteworthy. In the largest pedicle valve of *D. berwynensis*, which at 14 mm. in length is still smaller than the average length of the *D. flabellulum* valves, secondary costellae branch off from 5 costae near the margin ; and two secondaries also occur in each of two valves of the new subspecies, 6·5 and 8 mm. long respectively. This earlier occurrence of costellation in the sample is still exceptional in that it was found in only 2 out of 24 valves over 6·5 mm. long ; but the possibility remains that had the Bala shells attained the size of the *D. flabellulum* ones, a late costellate condition might have been more characteristic of them than a costate one.

Statistics assessing the relative growth of a number of morphological features in all three samples are given in Tables 16–21, 23, 24. Apart from the outline and relative length of its cardinalia, for which the derived coefficients of correlation (r) are not significant, *D. flabellulum* can be shown to differ importantly from the Bala shells in many ways. Thus, although all three stocks increased in the relative depth of their brachial valves at about the same rates, the inherent convexity (β) of *D. flabellulum* was significantly greater than that of the others ($p < ·001$). Similarly, the ventral muscle field of *D. flabellulum* extended anteriorly at a significantly faster rate ($p < ·01$) than that of the Bala *Dinorthis* (Table 17) but at the same time retained a subrectangular outline comparable, both in growth and residual proportions, with the other two (Table 18). The dental lamellae of both Bala samples also proved to be significantly longer ($·05 > p > ·02$) than those of *D. flabellulum* although for different reasons, because those of *D. berwynensis* grew at about the same rate but were inherently longer whereas those of the new subspecies extended anteriorly much more quickly relative to the increase in valve length. Finally, in the outline of the pedicle valve (Table 21) *D. flabellulum* is close to *D. berwynensis* in that both of them are inherently wider relative to length than *D. berwynensis angusta* ($p < ·001$). In contrast, a shallow sulcus, embracing between 5 and 9 costae antero-medianly, originated at a mean distance (with variance) of 5·8 mm. (0·44) and 6·1 mm. (0·821) anterior of the umbones of 8 and 24 pedicle valves of *D. berwynensis* and *D. berwynensis angusta* respectively. The difference is not significant and since no comparable feature was observed in *D. flabellulum*

it can at least be held that the pedicle valve of *D. berwynensis* in its total external morphology is intermediate between the other two samples. Except for the difference in ventral outline referred to above, the tables show that other distinctions between *D. berwynensis* and the new subspecies are limited to attributes of the brachial valves. A comparison of the relative growth of the dorsal interareas (Table 24) reveals that those of *D. berwynensis* extended anteriorly at a significantly slower pace than those of the new subspecies ($\cdot 05 > p > \cdot 02$) while the brachiophore bases of *D. berwynensis* were inherently shorter ($\cdot 05 > p > \cdot 02$) than those of the high Allt Ddu forms (Table 19). But in the early development of a fully differentiated cardinal process they are both quite different from *D. flabellulum*. Unfortunately, data for similar size ranges were not available, but only 5 out of 11 brachial valves of *D. flabellulum*, between 15 and 20 mm. long, bore a well developed crenulated myophore as well as a stout shaft ; whereas this condition had already been attained in 8 out of 8 and 4 out of 5 brachial valves, over 8 mm. long, of *D. berwynensis angusta* and *D. berwynensis* respectively.

The costate *Dinorthis* specimens from the Bala district are therefore quite distinct from *D. flabellulum* in their narrower costae, their sulcate pedicle valves, their shallower brachial valves, their well developed cardinal processes and their relatively shorter ventral muscle scars. These differences suggest that the Welsh samples are closely related to each other and the balance of morphological features confirms that this is so. But differences also exist between them—notably in the wider pedicle valve and the shorter dorsal interarea and brachiophore bases—and are important enough to warrant the erection of a new subspecies to embrace the high Allt Ddu forms.

Table 16

	A	B	C
$\bar{l}$ mm. (var. l) .	16·83 (16·693)	9·68 (16·401)	8·86 (13·28)
$\bar{dl}$ mm. (var. dl) .	1·64 (0·184)	1·33 (0·339)	1·45 (0·402)
r . .	0·699	0·936	0·774
a (var. a) . .	0·105 (0·00082)	0·1437 (0·00015)	0·174 (0·00044)

Table 16. Statistics of length of pedicle valve (l) and length of dental lamellae (dl) for 9 specimens of *Dinorthis flabellulum* (J. de C. Sowerby) (A), 19 of *D. berwynensis* (Whittington) (B) and 31 of *D. berwynensis angusta* subsp. nov. (C).

Table 17

	A	B	C
$\bar{l}$ mm. (var. l) .	16·15 (7·821)	8·8 (21·442)	8·24 (15·258)
$\bar{sc}$ mm. (var. sc)	7·87 (3·626)	3·36 (3·62)	3·1 (2·154)
r . .	0·804	0·905	0·959
a (var. a). .	0·6808 (0·00965)	0·4109 (0·00139)	0·3758 (0·00031)

Table 17. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for 19 specimens of *Dinorthis flabellulum* (J. de C. Sowerby) (A), 24 of *D. berwynensis* (Whittington) (B) and 35 of *D. berwynensis angusta* subsp. nov. (C).

TABLE 18

	A		B		C	
$\bar{l}$ mm. (var. l) .	8·05	(2·718)	3·75	(1·918)	3·11	(2·234)
$\bar{w}$ mm. (var. w) .	6·46	(2·207)	3·45	(1·272)	2·68	(1·184)
r . .	0·775		0·945		0·963	
$\log_e \bar{l}$ (var. $\log_e$ l) .	2·0651	(0·0411)	1·2581	(0·1274)	1·0311	(0·207)
$\log_e \bar{w}$ (var. $\log_e$ w) .	1·8397	(0·0517)	1·1877	(0·1014)	0·9094	(0·1528)
r_e . .	0·807		0·958		0·974	
α (var. α) .	1·122	(0·02308)	0·8921	(0·00595)	0·8592	(0·00115)

TABLE 18. Statistics of length (l) and maximum width (w) of the ventral muscle scar of 21 pedicle valves of *Dinorthis flabellulum* (A), 11 of *D. berwynensis* (Whittington) (B) and of 35 *D. berwynensis angusta* subsp. nov. (C).

TABLE 19

	A		B		C	
$\bar{l}$ mm. (var. l) .	19·16	(9·634)	7·86	(17·646)	6·22	(11·315)
$\bar{c}$ mm. (var. c) .	3·3	(0·24)	1·37	(0·438)	1·32	(0·436)
r . .	0·574		0·85		0·98	
$\log_e \bar{l}$ (var. $\log_e$ l) .	—		1·9446	(0·2517)	1·6993	(0·257)
$\log_e \bar{c}$ (var. $\log_e$ c) .	—		0·2001	(0·2094)	0·166	(0·2231)
r_e . .	—		0·866		0·982	
α (var. α) .	—		0·9121	(0·0104)	0·9318	(0·00103)

TABLE 19. Statistics of length of brachial valve (l) and length of brachiophores at their bases (c) for 8 specimens of *Dinorthis flabellulum* (J. de C. Sowerby) (A), 22 specimens of *D. berwynensis* (Whittington) (B) and 32 specimens of *D. berwynensis angusta* subsp. nov. (C).

TABLE 20

	A		B		C	
$\bar{l}$ mm. (var. l) .	3·4	(0·278)	1·43	(0·279)	1·32	(0·421)
$\bar{w}$ mm. (var. w) .	5·43	(0·168)	2·66	(0·725)	2·37	(1·283)
r . .	0·664		0·97		0·971	
$\log_e \bar{l}$ (var. $\log_e$ l) .	—		0·294	(0·1274)	0·1685	(0·2167)
$\log_e \bar{w}$ (var. $\log_e$ w) .	—		0·9293	(0·0979)	0·7606	(0·2053)
r_e . .	—		0·974		0·973	
α (var. α) .	—		0·8766	(0·00282)	0·9733	(0·00141)

TABLE 20. Statistics of length of brachiophores at their bases (l) and width of sockets (w) for 9 brachial valves of *Dinorthis flabellulum* (J. de C. Sowerby) (A), 16 of *D. berwynensis* (Whittington) (B) and 28 of *D. berwynensis angusta* subsp. nov. (C).

TABLE 21

	A	B	C
$\bar{l}$ mm. (var. l) .	17·17 (7·339)	5·79 (15·43)	6·53 (9·528)
$\bar{w}$ mm. (var. w) .	23·77 (12·186)	7·93 (21·624)	8·33 (14·269)
r . .	0·811	0·987	0·979
$\log_e \bar{l}$ (var. $\log_e$ l) .	2·8039 (0·0246)	1·5669 (0·3784)	1·7757 (0·2013)
$\log_e \bar{w}$ (var. $\log_e$ w) .	3·1576 (0·0217)	1·9232 (0·2949)	2·0267 (0·1863)
r_e . .	0·801	0·986	0·971
α (var α) .	0·9392 (0·01129)	0·8828 (0·00098)	0·9621 (0·00113)

TABLE 21. Statistics of length (l) and maximum width (w) of 30 pedicle valves of *Dinorthis flabellulum* (J. de C. Sowerby) (A), 24 of *D. berwynensis* (Whittington) (B) and 49 of *D. berwynensis angusta* subsp. nov. (C)

TABLE 22

	Number of costae		
	18–20	21–23	24–26
A	3	2	12
B	1(2)	2(9)	3(4)
C	0(0)	6(12)	5(13)

TABLE 22. The number of pedicle valves over 10 mm. long (and between 5 and 10 mm. long in brackets) of *Dinorthis flabellulum* (J. de C. Sowerby) (A), *D. berwynensis* (Whittington) (B), and *D. berwynensis angusta* subsp. nov. (C) bearing between 18 and 26 costae.

TABLE 23

	A	B	C
$\bar{l}$ mm. (var. l) .	16·08 (12·202)	7·61 (10·5)	6·68 (10·98)
$\bar{th}$ mm. (var. th)	3·86 (1·78)	2·25 (1·236)	2·54 (2·544)
r . .	0·555	0·862	0·942
$\log_e \bar{l}$ (var. $\log_e$ l) .	2·7545 (0·0459)	1·9459 (0·1672)	1·7891 (0·2199)
$\log_e \bar{th}$ (var. $\log_e$ th)	1·2940 (0·1133)	0·7017 (0·2183)	0·7664 (0·3315)
r_e . .	0·584	0·871	0·961
α (var. α) .	1·571 (0·04645)	1·143 (0·0105)	1·228 (0·00398)

TABLE 23. Statistics of length (l) and depth (th) of 37 brachial valves of *Dinorthis flabellulum* (J. de C. Sowerby) (A), 32 of *D. berwynensis* (Whittington) (B) and 31 of *D. berwynensis angusta* subsp. nov. (C).

TABLE 24

	A	B
$\bar{l}$ mm. (var. l) . .	8·4 (17·958)	7·08 (9·39)
$\bar{in}$ mm. (var. in) .	0·64 (0·098)	0·6 (0·0544)
r . . .	0·923	0·916
a (var. a) . .	0·07387 (0·00005)	0·7611 (0·00004)

TABLE 24. Statistics of length of brachial valve (l) and length of dorsal interarea (in) for 18 specimens of *Dinorthis berwynensis* (Whittington) (A) and 24 specimens of *D. berwynensis angusta* subsp. nov. (B).

Family PLECTORTHIDAE Schuchert & Le Vene 1929

Subfamily PLATYSTROPHIINAE Schuchert & Le Vene 1929

Genus ***PLATYSTROPHIA*** King 1850

TYPE SPECIES. *Terebratulites biforatus* Schlotheim by original designation of King (1850 : 106).

Platystrophia* cf. *sublimis Öpik

(Pl. 3, figs. 15–22)

DESCRIPTION. Strongly biconvex, subquadrate *Platystrophia* with the brachial valve just over two-thirds as long as wide and over one-half as deep as long, dorsal fold strong, high, less than two-thirds as wide as the valve is deep ; costae angular, covered with densely distributed pustules and numbering 2 or more commonly 3, in the ventral sulcus and 12 to 16, most commonly 15, on the flanks ; ventral interior with massive teeth, short receding dental lamellae and a subtriangular muscle field impressed on floor of the valve anterior of the umbo for just over one-third the length of the valve and just over one-half as wide as long ; cardinal process ridge-like, notothyrial platform and brachiophore supports obliterated by secondary shell deposition, adductor muscle impressions quadripartite about a low median ridge with the subtriangular anterior pair the larger.

MATERIAL (Figured).	length	width (mm.)
Incomplete internal mould of brachial valve (BB.29015)	21·0	—
Incomplete internal mould of pedicle valve (BB.29016)	27·0	—
Incomplete external mould of brachial valve (BB.29017)	—	—
Incomplete external mould of pedicle valve (BB.29018)	—	—
Incomplete external mould of pedicle valve (BB.29019)	—	—
Incomplete external mould of pedicle valve (BB.29020)	19·0	—
Internal and external mould of brachial valve (BB.29021–22)	5·5	9·5

HORIZON AND LOCALITIES. Gelli-grîn Group : BB.29018 from calcareous ashes exposed in the first crag on the south side of the head of the stream issuing from Craig y Gath ; other specimens from calcareous ashes cropping out immediately west of fence at south-east end of prominent Rhiwlas Limestone scarp, 500 ft. south-west of BM.1338.7, south side of Bryn Pig.

DISCUSSION. Moulds of *Platystrophia* occur sporadically in the ashes and limestones of the Gelli-grîn Group but are commonly so badly deformed that little information can be given at present on the morphological variability inherent to the stock. The pattern of radial ornamentation, however, affords some guide to the affinities of the shells and also suggests that the phylogenetic classification given

by McEwan (1920 : 383–404) requires some revision. Judging from the disposition of the costae within the ventral sulcus, the shells belong to her " biplicate (i.e. bicostate) group-subgroup A " (p. 389), in that a pair of submedian costae,presumably arising by dichotomy of a " nepionic " median costa, were characteristic of 5 ventral moulds. In 7 other moulds, however, 3 costae occupied the sulcus. In one valve the median costa is seen to have arisen by branching from the right submedian and in another the left submedian costa arose on the shoulder bounding the sulcus when the shell was a few millimetres long but during growth it became part of the floor of the sulcus ; for the remaining 5 moulds it was not possible to determine the origin of the third costa. McEwan (1920 : 407) has described a species, *P. trentonensis*, that is also characterized by the presence of 3 costae in the sulcus, although in this stock, and indeed, according to McEwan (1920 : 389), in all similarly ornamented *Platystrophia* (her subgroup B), the median costa arose last and by intercalation. In effect, if the current infrageneric segregation of *Platystrophia* based on the number and mode of origin of the costae within the sulcus were adopted for the Bala shells, three species would have to be recognized within what is certainly a homogeneous sample. Unfortunately such a procedure has been general practice. Thus Öpik (1930 : 105–108) has identified specimens of *Platystrophia* from the $C_{3\alpha}$ beds of Kohtla as *P. dentata* (Pander) or *P. sublimis* Öpik dependent on whether the ventral sulcus is occupied by 2 or 3 costae respectively. This association is reminiscent of the relationships within the Bala sample and although it is not yet known whether the third costa arose in a similar way, the Welsh and Baltic shells provisionally may be regarded as conspecific. It is noteworthy that in older Baltic rocks the bicostate group of *Platystrophia* is represented exclusively by the *P. dentata* type of shell because a similarly ornamented form, *P. precedens major* Williams, is recorded in the Derfel Limestone (see Whittington & Williams 1955 : 402) and in the Upper Llandeilo rocks of the Berwyn Dome (MacGregor 1961 : 184).

Subfamily RHACTORTHINAE nov.

Biconvex, dorsally sulcate plectorthids with hollow costellae, a subpentagonal ventral muscle field including a wide adductor scar not enclosed by the diductor lobes, a posteriorly crenulated cardinal process continuous with a dorsal median ridge and divergent brachiophore bases curving laterally to define the sockets.

Genus ***RHACTORTHIS*** nov.

Diagnosis. Subquadrate, biconvex shells with deep, subcarinate pedicle valve and less convex, sharply sulcate brachial valve ; radial ornamentation evenly multicostellate, broken by gross " growth lines ", costellae commonly arising by dichotomy and commonly hollow ; ventral interarea, straight, apsacline with wide open delthyrium, dorsal interarea short, straight, anacline, notothyrium open, occupied by posterior face of cardinal process ; shell probably impunctate.

Ventral interior with massive teeth, supported by short, receding, divergent dental lamellae posteriorly enclosing subpentagonal muscle field with wide, undifferentiated adductor scar, separating narrow, divergent, submedian diductor lobes which encroach onto a pair of subparallel *vascula media*, ventral pallial sinus incompletely

known but possibly saccate with subsidiary gonadal sac anterior of muscle field, between posterior portions of *vascula media*.

Dorsal interior with ridge-like cardinal process, thickened and posteriorly crenulated in adult stages of growth but always continuous with long median ridge ; brachiophores, short, rod-like, slightly divergent and embedded in pair of bases which curve laterally away from median plane to define the sockets, adductor scars situated posteriorly on either side of median ridge, just anterior of socket ridges ; *vascula media* and *myaria* diverging and branching from adductor field possibly as part of saccate pallial sinus pattern ; interiors of both valves with strongly raised concentric ridges corresponding to external breaks in forward growth of valves.

Type species. *Rhactorthis crassa* sp. nov. from the Gelli-grîn Group, Bala.

Discussion. The new genus, specimens of which are fairly common in the Gelli-grîn Group of the Bala district and are also known to occur in the Longvillian strata of the Welsh Borderland and the Lake District, has hitherto passed as a " dalmanellid " *s.l.* (e.g. Bancroft 1928 : 489) or an orthid *s.s.* (e.g. *Orthis melmerbiensis* Reed 1910 : 296). The arrangement of the brachiophores is admittedly like that of the dalmanellids *Bancroftina* Sinclair and *Eodalmanella* Havlíček, but fragments of shell found adherent to some of the Welsh moulds were all impunctate and as an orthaceid it is so distinctive that it can only be accommodated provisionally within a new subfamily of the Plectorthidae. There are certainly features which are also characteristic of various plectorthid genera. Dichotomous ribbing is typical of many species of *Plectorthis* Hall & Clarke ; hollow costellae were developed in *Doleroides* Cooper ; the ventral muscle field, with the wide adductor scar, is like that of *Mimella* Cooper ; and, apart from the sharp dorsal sulcus, the outline and profile of the new genus are also reminiscent of *Mimella*. The brachiophore bases of all plectorthids, however, converge on to the notothyrial platform or even the median ridge and the sockets are concomitantly defined by strong fulcral plates. By contrast, the brachiophore bases of the new genus diverge to lie more or less parallel with the hinge-line and in this attitude they not only give support to the brachiophores but also serve as confining walls to the sockets. This disposition is rare even among those dalmanellaceids with divergent brachiophore bases. It is at present unique among the orthaceids and until more is known about the development of the plectorthid cardinalia it seems best to segregate *Rhactorthis* from all other contemporary orthaceids at least at the subfamilial level.

Rhactorthis crassa gen. et sp. nov.
(Pl. 4, figs. 1–6 ; Text-fig. 8)

Diagnosis. Subcircular, unequally biconvex *Rhactorthis* with sulcate brachial valve, nearly three-quarters as long as wide, just over one-fifth as deep as long, and high pedicle valve nearly two-fifths as deep as long, radial ornamentation multicostellate but interrupted by thick, irregularly spaced concentric zones of negligible forward growth, costellae, commonly hollow and about 3 per mm. at a distance of 5 mm. anterior of dorsal umbo, tending to arise by dichotomous branching

with secondary externals rarely appearing in Sectors I to IV during early growth stages ; ventral muscle scar subpentagonal becoming relatively longer than wide during adult stages of growth and extending anteriorly for just over one-third the length of pedicle valve, submedian diductor lobes not projecting very much forward of wide adductor scar ; brachiophore bases widely splayed to define sockets, less than one-sixth as long as brachial valve and about two-fifths as long as wide, dorsal adductor scars elongate, extending anteriorly for about one-half of brachial valve on either side of median ridge.

		length	width (mm.)
Holotype.	Internal mould of brachial valve (BB.28878)	3·5	5·0
Paratypes.	Deformed external mould of brachial valve (BB.28879)	6·5	10·0
	Incomplete external moulds of conjoined valves (BB.28880)	—	—
	Deformed internal mould of pedicle valve (BB.24542)	9·5	10·5
	External and internal moulds of pedicle valve (BB.28881–82)	8·5	—
	Internal mould of brachial valve (BB.29028)	8·5	—
	Internal mould of pedicle valve (BB.28883)	8·5	—
	Internal mould of brachial valve (BB.28884)	2·3	4·0
	Incomplete external mould of pedicle valve with adherent shell (BB.28885)	—	—

Horizon and localities. Gelli-grîn Group : BB.28879–80, BB.29028, BB.28884 from calcareous ashes exposed on north side of the southern Rhiwlas Limestone outlier on Creigiau Bychain ; BB.28883, BB.28885 from calcareous ash outcrops on the east side of the central Rhiwlas Limestone outlier, Creigiau Bychain ; BB.28878, BB.24542 from calcareous ash crags beginning 75 ft. south of the east end of ruined buildings in Ffridd Bach, south of Maes-meillion ; BB.28881–82 calcareous ash crags in field 600 ft. south-east of Bryn-briglas.

Table 25

$\bar{l}$ mm. (var. l) .	3·9	(3·872)
$\bar{w}$ mm. (var. w).	5·43	(5·457)
r . .	0·933	
$\log_e \bar{l}$ (var. $\log_e$ l) .	1·2474	(0·2271)
$\log_e \bar{w}$ (var. $\log_e$ w) .	1·6069	(0·1699)
r_e . .	0·945	
α (var. α) .	0·865	(0·004)

Table 25. Statistics of length (l) and maximum width (w) of 22 brachial valves of *Rhactorthis crassa* gen. et sp. nov.

TABLE 26

$\bar{l}$ mm. (var. l) .	6·1	(3·586)
$\bar{c}$ mm. (var. c) .	1·07	(0·127)
r . .	0·889	
a (var. a). .	0·1882	(0·00073)

TABLE 26. Statistics of length (l) and length of cardinalia (c) of 12 brachial valves of *Rhactorthis crassa* gen. et sp. nov.

TABLE 27

$\bar{l}$ mm. (var. l) .	1·08	(0·144)
$\bar{w}$ mm. (var. w) .	2·65	(0·547)
r . .	0·813	
a (var. a). .	1·949	(0·16103)

TABLE 27. Statistics of length (l) and maximum width (w) of the cardinalia of 10 brachial valves of *Rhactorthis crassa* gen. et sp. nov.

TABLE 28

$\bar{l}$ mm. (var. l) .	8·14	(8·131)
$\bar{m}$ mm. (var. m) .	2·87	(1·702)
r . .	0·967	
a (var. a). .	0·4575	(0·0017)

TABLE 28. Statistics of length (l) and length of ventral muscle field (m) of 10 pedicle valves of *Rhactorthis crassa* gen. et sp. nov.

TABLE 29

$\bar{l}$ mm. (var. l) .	3·15	(1·565)
$\bar{w}$ mm. (var. w) .	2·78	(0·858)
r . .	0·964	
$\log_e \bar{l}$ (var. $\log_e$ l) .	1·0744	(0·1459)
$\log_e \bar{w}$ (var. $\log_e$ w) .	0·9698	(0·1053)
r_e . .	0·964	
α (var. α) .	0·8495	(0·0051)

TABLE 29. Statistics of length (l) and maximum width (w) of the ventral muscle field of 12 pedicle valves of *Rhactorthis crassa* gen. et sp. nov.

DISCUSSION. Most of the relevant data concerning the variability of the new species have been set out in Tables 25–29 which show that the growth of the brachial valves tended to accelerate in length relative to width in adult shells and that the ventral muscle field which was initially wider than long ultimately expanded anteriorly at a faster rate than its lateral encroachment along the valve floor. The strongly convex profiles of both valves are reflected in the mean percentage depth relative to length of 22·2 (variance 8·2) for 6 brachial valves and of 39 (range 36 to 41) for 3 pedicle valves. The radial ornamentation is rather fine with counts of 2, 3 or 4 ribs per mm. 5 mm. anterior of the dorsal umbones of 1, 5 and 1 specimens respectively. At the 2 mm. growth stage, 14–18 costae ornament the brachial valve with the secondary costellae, 1ā, 2ā, 3ā, 4ā and 4a° also appearing in 7/12, 10/12, 10/12, 2/10 and 1/10 specimens respectively. 3ā arose earlier than 1ā and 2ā

in 6/8 and 5/8 specimens respectively. The dorsal adductor scars are not deeply impressed but appear to be quite variable in their percentage length measured from the umbo, relative to the length of the brachial valve which averaged 51 (range 40 to 62) in 4 internal moulds.

The only other described species known to be congeneric with *R. crassa* is *R. melmerbiensis* (Reed 1910 : 296) but although only a few specimens of this latter species were available for study they can immediately be distinguished from *R. crassa* in the strongly carinate pedicle valve which is consequently deeper with an average percentage depth relative to the length of 3 valves of 45 (range 42 to 56) and in the correspondingly deeper but wider dorsal sulcus. *R. melmerbiensis* may also ultimately prove to have a relatively wider brachial valve which is certainly more semi-oval than the new species but internally the differences appear to be negligible.

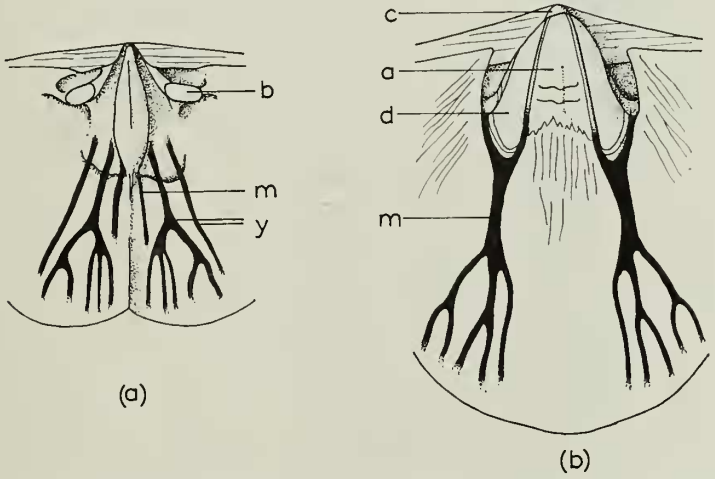

Fig. 8. The dorsal interior (a) and the ventral internal mould (b) of *Rhactorthis crassa* gen. et sp. nov., ×5 approx.: *a*, adductor scar ; *b*, brachiophore ; *c*, pedicle callist ; *d*, diductor scar ; *m*, *vascula media* ; *y*, *vascula myaria*.

Family SKENIDIIDAE Kozlowski 1929

Genus ***SKENIDIOIDES*** Schuchert & Cooper 1931

Type species. *Skenidioides billingsi* Schuchert & Cooper by original designation of Schuchert & Cooper (1931 : 71).

Skenidioides* cf. *costatus Cooper

(Pl. 4, figs. 7–14)

Description. Semi-oval *Skenidioides* with a subpyramidal pedicle valve about three-fifths as long as wide and one-half as deep as long and a very gently convex brachial valve sharply depressed about a median sulcus ; surface essentially costate with, in the pedicle valve, a wide median costa about 0·5 mm. in wavelength 2 mm.

anterior of the umbo flanked on either side by up to 8 rounded costae with a wavelength of about 0·3 mm., costellae arising early especially in the first three sectors ; spondylium, shallow, mostly free but supported umbonally by a thickened deposit of secondary shell commonly prolonged as a ridge along the anterior surface of the spondylium and especially along the valve floor for almost one-quarter the length of the valve ; ventral pallial sinus pattern digitate ; cardinal process thin, ridge-like and continuous with the median septum which is subtriangular in outline with the apex just anterior of the mid-line, brachiophores slender, with bases convergent on to the median septum at about one-third the valve length anterior of the umbo, sockets small and defined by fulcral plates ; dorsal adductor field as a pair of lanceolate impressions divided by the septum and extending anteriorly for almost two-thirds the length of the brachial valve.

Material (Figured).	length	width (mm.)
Internal mould of brachial valve (BB.28917)	2·8	3·8
Internal mould of pedicle valve (BB.28918)	4·0	5·5
Incomplete internal mould of brachial valve (BB.28919)	—	—
Incomplete internal mould of pedicle valve (BB.28921)	4·7	—
Incomplete external mould of brachial valve (BB.28920)	—	—
External mould of pedicle valve (BB.28922)	2·3	4·5
Deformed internal mould of brachial valve (BB.24548)	4·5	7·7
Deformed internal mould of pedicle valve (BB.28924)	4·5	7·2

Table 30

$\bar{l}$ mm. (var. l) .	2·48	(0·977)
$\bar{w}$ mm. (var. w) .	4·15	(1·536)
r . .	0·938	
a (var. a). .	1·254	(0·0094)

Table 30. Statistics of the length (l) and maximum width (w) of 22 pedicle valves of *Skenidioides* cf. *costatus* Cooper.

Table 31

$\bar{l}$ mm. (var. l) .	2·73	(1·264)
$\bar{th}$ mm. (var. th)	1·36	(0·378)
r . .	0·808	
a (var. a). .	0·547	(0·0104)

Table 31. Statistics of the length (l) and maximum thickness (th) of 12 pedicle valves of *Skenidioides* cf. *costatus* Cooper.

Table 32

$\bar{l}$ mm. (var. l) .	3·05	(0·825)
$\bar{c}$ mm. (var. c) .	1·01	(0·102)
r . .	0·932	
a (var. a). .	0·352	(0·0014)

Table 32. Statistics of the length of 14 brachial valves (l) and their cardinalia (c) of *Skenidioides* cf. *costatus* Cooper.

Horizons and localities. Gelli-grîn Group : BB.24548 from calcareous ashes exposed in Ffridd Bach immediately south of Maes-meillion Farm ; all other specimens from calcareous ashes exposed on the east side of the central outlier of Rhiwlas Limestone on Creigiau Bychain.

Discussion. *Skenidioides* is fairly common in the Gelli-grîn Group and is quite distinctive, especially in its radial ornamentation. As can be seen from Tables 30–32, the subpyramidal pedicle valve was inherently wider than long and this was maintained throughout growth as was the relative depth of the valve. The radial ornamentation consists essentially of up to 17 costae with the median costa, forming the crest of the pedicle valve, having a mean wavelength of 0·5 mm. (range 0·45–0·65 mm.) compared with a mean wavelength of 0·3 mm. (range 0·2–0·35 mm.) for the lateral costae in 4 pedicle valves. But in pedicle valves between 2·0 and 3·0 mm. long the costellae 1a°, 2a°, 3ā, 3a° and 4a° split off from their parent primaries in 5/8, 7/8, 2/8, 5/8 and 2/7 valves respectively with 2a° invariably arising before 3a° and 4a° and even before 1a° in 5/7 valves. Internally, the most distinctive feature is the well developed cardinalia dominated by the strong brachiophore bases which converge onto the median septum of the brachial valve at almost one-third the length of the valve anterior of the dorsal umbo, a proportion that was maintained throughout growth.

These *Skenidioides* are at present inseparable from *S. costatus* Cooper (1956 : 493) from the Edinburg formation of Virginia. Certainly the relative proportions representing shell outline, profile and size of internal features of the American type specimens are all well within the ranges of those assessed for the Welsh stock, and in radial ornamentation, even to details of secondary branching, the two stocks are identical.

Family CREMNORTHIDAE nov.

Diagnosis. Biconvex, costellate and dorsally sulcate orthaceids with short, curved interareas and unmodified delthyrium and notothyrium ; ventral muscle field subtriangular with wide adductor scar, dental lamellae, if present, short and receding ; cardinalia consisting of stout, trilobed cardinal process continuous with high, blade-like median septum, subtriangular in outline and extending to anterior margin, and pair of short, divergent brachiophores with bases curved laterally to define pair of semi-oval sockets.

Genus *CREMNORTHIS* nov.

Diagnosis. Subcircular, biconvex shells with deep, subcarinate pedicle valve and strongly convex and sulcate brachial valve so that commissure is sharply sulcate antero-medianly and curved laterally with convex arcs facing dorsally ; radial ornamentation fascicostellate with angular costae and costellae ; ventral interarea curved, apsacline with open, narrow delthyrium ; dorsal interarea short, curved, anacline, notothyrium filled by cardinal process; shell probably impunctate.

Ventral interior with obliquely disposed teeth ankylosed to floor of valve by thick deposits of secondary shell rather than discrete dental lamellae, pedicle callist well developed ; muscle field not extending much beyond umbonal cavity, subtriangular in outline with wide median adductor scar separating pair of diductor scars each of which consists of narrow, ventrally facing submedian lobe enclosed anteriorly by *vasculum medium* and lateral lobe impressed on the side of umbonal cavity ; pallial sinus pattern unknown except for a pair of divergent *vascula media*.

Dorsal interior with cardinalia dominated by massive cardinal process standing well above hinge-line and trilobed in arrangement with median crest separating ventral parts of areas for diductor insertion ; brachiophores, short, obliquely disposed and continuous with bases which curve laterally to define a pair of semi-elliptical sockets ; cardinal process continuous with blade-like median septum which extends to anterior margin and which must have been sufficiently high almost to make contact with pedicle valve along its antero-median half ; dorsal adductor field elongately oval, quadripartite impressed on either side of septum just anterior of cardinalia and further divided by narrowly divergent *vascula myaria*.

Type species. *Cremnorthis parva* sp. nov. from the Gelli-grîn Group.

Discussion. The new genus is at present represented solely by the type species which itself is known only from a small number of internal and external moulds so that no original shell material has been recovered to determine whether the test was punctate or impunctate. Despite the coarseness of the Gelli-grîn calcareous ashes, however, the puncta of all dalmanellaceids recovered from the deposits were filled with ferric oxides and clays which adhered to the internal moulds as fine granules and the invariable absence of these suggests that the species was impunctate in the orthaceid manner : in any event it is sufficiently distinctive to be recognized without recourse to the condition of the shell. Among the orthaceids, closest comparison can be drawn with the contemporary *Phragmorthis* Cooper (1956 : 508–510) in the general aspect of the shell, in the nature of the ventral muscle field and especially in the presence of a high median septum. This similarity, however, may be an expression of convergence for the brachiophore bases do not converge on to the median septum as in *Phragmorthis* which also lacks the elaborate cardinal process and fascicostellate ornamentation of *Cremnorthis*. Indeed, in respect of most features, the new genus has more in common with certain Devonian dalmanellaceids like *Prokopia* (Havlíček 1956 : 118) although it differs, apart from its probable impunctate test, in both the style of ornamentation and the structure of the cardinal process, and the likeness is more probably the result of homeomorphy than affinity.

Cremnorthis parva gen. et sp. nov.

(Pl. 4, figs. 15–23 ; Text-fig. 9)

Diagnosis. Subrectangular, strongly biconvex *Cremnorthis* with medianly sulcate brachial valve over two-thirds as long as wide and about three-tenths as deep as long and subcarinate pedicle valve nearly one-half as deep as long ; ventral interarea curved about one-tenth as long as pedicle valve and twice as long as dorsal interarea ; radial ornamentation fascicostellate with sharply angular costae and costellae about 4 per mm. at 2 mm. anterior of dorsal umbo, sectors I and II occurring within dorsal sulcus, external secondary costellae common in sectors II to V ; pedicle callist well developed, less than one-tenth as long as pedicle valve, ventral subtriangular muscle scar almost as long as wide and extending anteriorly for just over one-third the length of valve ; brachiophore bases widely splayed and strong, almost one-fifth as long as brachial valve and about two-fifths as long as wide ; dorsal median septum attaining a height of almost one-third the length of brachial valve in anterior half of its extent ; dorsal adductor scars impressed on either side of septum just anterior of brachiophore bases and extending anteriorly for almost three-quarters the length of valve.

		length	width (mm.)
Holotype.	Internal mould of brachial valve (BB.28923)	2·3	—
Paratypes.	Internal mould of brachial valve (BB.28896)	3·0	4·0
	Internal mould of pedicle valve (BB.28897)	3·6	4·2
	External mould of brachial valve (BB.28898)	3·2	3·8
	External mould of pedicle valve (BB.28899)	1·2	1·9
	External mould of conjoined valves, ventral aspect (BB.28900)	3·5	—

Horizon and locality. Gelli-grîn Group : calcareous ashes exposed above limestone in the old quarry, 1,100 ft. west-south-west of Gelli-grîn Farm.

Discussion. The new species is at least generically distinguishable from contemporary brachiopods so that only some aspects of the diagnosis need further discussion. The mean percentage length relative to width, and depth relative to length of 6 dorsal external moulds (with variance) were respectively 68·8 (88·6) and 26·8 (20·6). The subcarinate pedicle valves were more strongly convex with a mean percentage depth relative to length (with variance) in 7 specimens of 48·1 (58·5). In the ventral internal moulds the conspicuous, narrow pedicle callist had a mean percentage length relative to the length of 4 specimens of 8·5 (range 8 to 9) while in 5 specimens the mean percentage length of the muscle field anterior to the umbo relative to the length of the valve and to its maximum width in ventral aspect were (with variances) 35 ·0 (39·0) and 95·6 (24·2) respectively. The robust

cardinalia formed prominent holes in the dorsal internal moulds and in 9 specimens the mean percentage length of the brachiophore bases relative to valve length (with variance) was 18·2 (11·13) while in 8 moulds the mean percentage length of the brachiophore bases relative to the maximum width of the sockets was 40·9 (variance 25·86).

The fascicostellate pattern is quite distinctive. In 3 brachial valves, 4 costellae occurred within 1 mm. at 2 mm. from the umbo and this order of wavelength is typical of the radial ornamentation except for a broad median costa occupying the crest of the pedicle valve. The pattern in the right halves of the brachial valves is typically 1, 2, 2a°, 3, 3a°, with 1ā, 2ā and 3ā occurring in 2/6, 3/6 and 2/4 specimens respectively, so that external secondary costellae are relatively well developed in the second and third sectors.

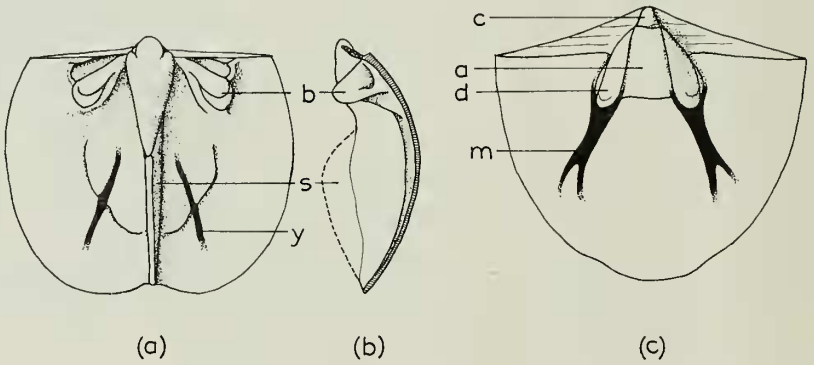

FIG. 9. The ventral (a) and lateral (b) aspects of a dorsal interior and the ventral internal mould (c) of *Cremnorthis parva* gen. et sp. nov., ×10 approx.: *a*, adductor scar ; *b*, brachiophore ; *c*, pedicle callist ; *d*, diductor scar ; *m*, *vascula media* ; *s*, septum ; *y*, *vascula myaria*.

Superfamily DALMANELLACEA Schuchert & Le Vene 1929

Family DALMANELLIDAE Schuchert & Le Vene 1929

Genus ***DALMANELLA*** Hall & Clarke 1892

TYPE SPECIES. *Orthis testudinaria* Dalman by original designation of Hall & Clarke (1892 : 205).

Dalmanella modica sp. nov.

(Pl. 4, figs. 24, 25 ; Pl. 5, figs. 1–7)

DIAGNOSIS. Subcircular, unequally biconvex *Dalmanella* with sulcate brachial valve about three-quarters as long as wide and almost one-fifth as deep as long and evenly convex pedicle valve just over one-third as deep as long ; radial ornamentation costellate with modal count of 3 costellae per mm., 5 mm. anterior

of dorsal umbo, external secondary branching poorly developed in sectors I to IV ; dental lamellae divergent, extending anteriorly for just over one-fifth the length of pedicle valve, teeth strong ; adult ventral muscle field subcordate in outline slightly narrower than long with submedian diductor scars extending forward of umbo for less than one-third the length of pedicle valve and not enclosing broad median adductor scar ; adult cardinalia consisting of undifferentiated bilobed cardinal process and rod-like brachiophores supported by a pair of subparallel bases, extending forward for about one-fifth the length of brachial valve, and a pair of widely divergent socket plates, almost twice as wide as brachiophore bases are long ; median ridge short, fading anteriorly into broad internal crest of sulcus, and dividing adductor field into a pair of suboval scars about one-half as long as brachial valve ; pallial sinus patterns unknown.

		length	width (mm.)
Holotype.	Internal mould of conjoined valves (BB.28960)	12·0	14·0
Paratypes.	External and internal moulds of pedicle valve (BB.28961–62)	7·0	7·0
	Internal mould of brachial valve (BB.29029)	7·8	9·1
	Internal mould of brachial valve (BB.29131)	8·5	9·5
	External and internal moulds of pedicle valve (BB.28963–64)	10·0	11·0
	External mould of brachial valve (BB.24603)	6·0	7·5
	External mould of brachial valve (BB.28966)	9·5	11·5
	External mould of brachial valve (BB.28967)	10·0	13·7

Horizon and localities. Gelli-grîn Group ; BB.28960, BB.24603 from calcareous ash crags beginning 75 ft. south of the east end of ruined buildings in Ffridd Bach, south of Maes-meillion ; BB.28961–62 calcareous ashes exposed on the east side of the central outlier of Rhiwlas Limestone, Creigiau Bychain ; BB.29029, BB.29131, BB.28963–64 calcareous ashes cropping out on the north side of the track leading from Gelli-grîn Farm, 1,000 ft. west-south-west of the farm, BB.28966–67 calcareous ash crags 700 ft. west-north-west of BM.1338.7, south side of Bryn Pig.

Discussion. Isolated valves of *Dalmanella* are fairly common in the Gelli-grîn Group and were referred by Bancroft (1945 : 193) to three distinct species—*D. horderleyensis* (Bancroft), *D. indica* (Whittington) and *D. lepta* (Bancroft). The last species was founded on immature shells and is conspecific with *D. indica* so that one would anticipate *Dalmanella* from the Bala district as belonging to two distinct

morphological assemblages. All the moulds recovered however, are the remains of a homogeneous group which is unlike any known *Dalmanella* in a number of details and is accordingly described as a new species, *Dalmanella modica*.

In his account of the generic features of *Wattsella* (now accepted as synonymous with *Dalmanella*), Bancroft (1945 : 190) laid great emphasis on the co-existence of " normal " and " progressive " forms characterized by the predominance of externally and internally branching costellae respectively. Bancroft clearly believed that these two groups merited supra-specific recognition and although other studies (Williams & Wright, 1963 : 20) suggest such procedure to be unnecessary the segregation into normal and progressive stocks is a convenient guide to *Dalmanella* taxonomy. Thus, Table 33 shows the new species to differ significantly ($p < \cdot 01$) from *D. horderleyensis* in the late origin of 3a° and 4b° in the manner comparable with *D. indica* (and *D. lepta*). But it also differs from these two ($p < \cdot 01$) in the early development of 2a°, a characteristic it shares with *D. horderleyensis*. This comparison of course does not imply that the Gelli-grîn shells were transitional between two species groups because patterns of branching are known to have been developed independently of one another in different sectors. On balance then, *D. modica* may be regarded as a progressive form as it also is in the rather fine texture of its costellate ornamentation because at a distance of 5 mm. anterior of the dorsal umbo, 2, 3 or 4 costellae per mm. were counted in 2, 17 and 14 brachial valves of *D. modica* compared with 0, 15 and 11 valves of *D. indica* and 9, 4 and 0 of *D. horderleyensis*.

TABLE 33

		A	B	C
1 ā ī)	1 b̄ . .	3/6 (1)	0/14 (1)	0/4 (1)
1 b̄)	1 ā . .	5/7 (1)	11/11	4/6
2 b̄ ī)	2 ā . .	0/4	3/3	0/2
2 c̄)	2 a° . .	1/6	5/5	0/2
3 ā 1ā)	3 a° . .	9/14 (1)	19/23	3/25 (1)
3 c̄)	3 a° . .	10/15 (1)	18/22	2/23 (2)
3 b̄ ī)	3 c̄ . .	3/10 (3)	3/8 (4)	3/3 (1)
3 ā īā)	3 ā 2̄ . .	11/11 (3)	7/8 (4)	2/5
4 b̄)	4 b° . .	15/19 (1)	11/15 (3)	2/15
4 ā ī°)	4 ā ī ā. .	4/8	0/7	—
4 ā ī°)	4 b̄ ī . .	6/6	0/5	—
4 ā īā)	4 b° . .	5/9 (1)	2/7	—
3 ā īā)	2 ā ī . .	3/9 (2)	5/14	—
3 ā īā)	2 a° . .	10/12	12/12	0/1

TABLE 33. The proportions of the earlier insertion of 14 costellae relative to 14 others (with the number of valves in which both costellae originated at the same growth stage in brackets) for samples of *Dalmanella modica* sp. nov. (A), *Dalmanella indica* (Whittington) (B), and *Dalmanella horderleyensis* (Bancroft) (C).

TABLE 34

	A		B	
$\bar{l}$ mm. (var. l)	4·91	(8·773)	7·98	(8·024)
$\bar{w}$ mm. (var. w)	6·53	(14·275)	10·23	(10·417)
r	0·985		0·933	
$\log_e \bar{l}$ (var. $\log_e$ l)	1·436	(0·3105)	2·0176	(0·1185)
$\log_e \bar{w}$ (var. $\log_e$ w)	1·7319	(0·2889)	2·2776	(0·0953)
r_e	0·989		0·992	
α (var. α)	0·9646	(0·00064)	0·8968	(0·00075)

TABLE 34. Statistics of length (l) and maximum width (w) of 34 brachial valves of *Dalmanella modica* sp. nov. (A) and of 19 brachial valves of *Dalmanella indica* (Whittington) (B).

TABLE 35

	A		B	
$\bar{l}$ mm. (var. l)	7·09	(2·615)	8·53	(5·075)
$\bar{th}$ mm. (var. th)	1·33	(0·194)	1·55	(0·314)
r	0·863		0·929	
$\log_e \bar{l}$ (var. $\log_e$ l)	1·9333	(0·0507)	2·1097	(0·0677)
$\log_e \bar{th}$ (var. $\log_e$ th)	0·233	(0·1044)	0·3767	(0·1231)
r_e	0·867		0·917	
α (var. α)	1·435	(0·03007)	1·348	(0·01807)

TABLE 35. Statistics of length (l) and thickness (th) of 19 brachial valves of *Dalmanella modica* sp. nov. (A) and of 18 brachial valves of *Dalmanella indica* (Whittington) (B).

TABLE 36

	A		B	
$\bar{l}$ mm. (var. l)	5·13	(10·44)	8·71	(3·218)
$\bar{c}$ mm. (var. c)	1·07	(0·369)	1·49	(0·127)
r	0·938		0·845	
$\log_e \bar{l}$ (var. $\log_e$ l)	1·4678	(0·3345)	2·1439	(0·0411)
$\log_e \bar{c}$ (var. $\log_e$ c)	0·0767	(0·2813)	0·371	(0·0555)
r_e	0·949		0·882	
α (var. α)	0·9171	(0·00209)	1·162	(0·01364)

TABLE 36. Statistics of length of brachial valves (l) and length of cardinalia (c) of 42 specimens of *Dalmanella modica* sp. nov. (A) and of 24 specimens of *Dalmanella indica* (Whittington) (B).

TABLE 37

	A		B	
$\bar{l}$ mm. (var. l)	1·2	(0·271)	1·45	(0·134)
$\bar{w}$ mm. (var. w)	2·17	(0·92)	2·81	(0·246)
r	0·841		0·788	
$\log_e \bar{l}$ (var. $\log_e$ l)	0·096	(0·1725)	0·3405	(0·0621)
$\log_e \bar{w}$ (var. $\log_e$ w)	0·6855	(0·1784)	1·0179	(0·0306)
r_e	0·842		0·81	
α (var. α)	1·017	(0·01368)	0·702	(0·00891)

TABLE 37. Statistics of length (l) and maximum width (w) of the cardinalia of 24 brachial valves of *Dalmanella modica* sp. nov. (A) and of 21 brachial valves of *Dalmanella indica* (Whittington) (B).

TABLE 38

	A		B	
$\bar{l}$ mm. (var. l)	7·74	(4·506)	8·72	(3·237)
$\bar{sc}$ mm. (var. sc)	3·84	(0·902)	4·53	(1·071)
r	0·918		0·921	
a (var. a)	0·4474	(0·00165)	0·5753	(0·00279)

TABLE 38. Statistics of length of brachial valve (l) and extension of adductor scars anterior of the umbo (sc) of 21 specimens of *Dalmanella modica* sp. nov. (A) and of 20 specimens of *Dalmanella indica* (Whittington) (B).

TABLE 39

	A		B	
$\bar{l}$ mm. (var. l)	7·1	(8·962)	6·49	(7·689)
$\bar{th}$ mm. (var. th)	2·45	(0·846)	1·93	(0·864)
r	0·929		0·922	
a (var. a)	0·3072	(0·00129)	0·3351	(0·00168)

TABLE 39. Statistics of length (l) and thickness (th) of 12 pedicle valves of *Dalmanella modica* sp. nov. (A) and of 12 pedicle valves of *Dalmanella indica* (Whittington) (B).

TABLE 40

	A		B	
$\bar{l}$ mm. (var. l)	5·76	(6·941)	6·92	(6·336)
$\bar{sc}$ mm. (var. sc)	1·82	(0·853)	2·34	(1·171)
r	0·959		0·969	
$\log_e \bar{l}$ (var. $\log_e$ l)	1·5693	(0·3632)	1·8724	(0·1239)
$\log_e \bar{sc}$ (var. $\log_e$ sc)	0·484	(0·2295)	0·7495	(0·2013)
r_e	0·969		0·962	
α (var. α)	0·795	(0·00257)	1·275	(0·00638)

TABLE 40. Statistics of length of pedicle valve (l) and length of ventral muscle field (sc) of 17 specimens of *Dalmanella modica* sp. nov. (A) and of 21 specimens of *Dalmanella indica* (Whittington) (B).

TABLE 41

	A		B	
$\bar{l}$ mm. (var. l)	1·83	(0·826)	2·34	(1·211)
$\bar{w}$ mm. (var. w)	1·77	(0·603)	2·27	(0·634)
r	0·911		0·966	
$\log_e \bar{l}$ (var. $\log_e$ l)	0·4939	(0·2207)	0·7503	(0·1997)
$\log_e \bar{w}$ (var. $\log_e$ w)	0·4827	(0·1766)	0·7618	(0·1159)
r_e	0·924		0·975	
α (var. α)	0·8971	(0·00905)	0·7619	(0·00159)

TABLE 41. Statistics of length (l) and maximum width (w) of the ventral muscle field of 15 specimens of *Dalmanella modica* sp. nov. (A) and of 20 specimens of *Dalmanella indica* (Whittington) (B).

TABLE 42

	A		B	
$\bar{l}$ mm. (var. l)	6·65	(7·393)	6·92	(6·336)
$\bar{dl}$ mm. (var. dl)	1·39	(0·254)	1·51	(0·36)
r	0·947		0·935	
a (var. a)	0·1854	(0·00175)	0·2383	(0·00038)

TABLE 42. Statistics of length of pedicle valve (l) and anterior extension of dental lamellae (dl) of 22 specimens of *Dalmanella modica* sp. nov. (A) and of 21 specimens of *Dalmanella indica* (Whittington) (B).

In other morphological features too, the new species is superficially like *D. indica*, a sample of which was obtained from the type locality (Bancroft 1945 : 195) for comparative purposes. The results of nine analyses of relative growth of both species are given in Tables 34–42. In the outline and profile of the brachial valves, the relative length of the cardinalia, the profile of the pedicle valve and the outline of the ventral muscle scar, the two samples show no noteworthy differences in either growth ratios or inherent proportions. The increase in width of the cardinalia (that is the lateral expansion of the fulcral plates) was, however, significantly faster in *D. modica* than in *D. indica* ($\cdot02 > p > \cdot01$) while the anterior migration of the dorsal adductor scars of *D. modica* was significantly slower ($\cdot05 > p > \cdot02$). Discernible differences also occurred in the pedicle valves. Thus, although the outlines of the ventral muscle scars were similar, that of *D. modica* did not extend anteriorly as fast as that of *D. indica* ($p < \cdot001$) and so was absolutely shorter relative to the valve throughout growth as were also the dental lamellae of *D. modica* ($\cdot05 > p > \cdot02$). Despite many similarities then the Gelli-grîn shells are quite distinct from *D. indica* especially in the early occurrence of external branching in the second sector of the brachial valve, in the fast lateral growth of the fulcral plates relative to the forward growth of the supporting plates and in the slower

anterior expansion of the ventral muscle field, the dental lamellae and the dorsal adductor scars relative to the growth of the shell.

Genus *HOWELLITES* Bancroft 1954

Diagnosis (emended). Subcircular, unequally biconvex to plano-convex shells with sulcate brachial valve ; radial ornamentation finely costellate with first to third order costellae branching internally more commonly than externally. Ventral interarea long, curved and apsacline with open delthyrium ; dorsal interarea short curved, anacline, notothyrium filled by cardinal process ; shell punctate.

Ventral interior with large teeth supported by well developed dental lamellae ; muscle field subtriangular to bilobed in outline with submedian diductor lobes not enclosing median adductor scar ; ventral pallial sinus pattern lemniscate, *vascula media* slightly divergent and greatly divided.

Dorsal interarea with stout undifferentiated bilobed cardinal process ; brachiophores short, rod-like with their bases slightly to greatly divergent relative to their tops, fulcral plates sporadically developed ; dorsal adductor scar quadripartite, elongately oval ; pallial sinus pattern lemniscate.

Type species. *Resserella* (*Howellites*) *striata* Bancroft.

Discussion. The taxonomic status of *Howellites*, which has been fully reviewed by Williams & Wright, 1963, may be summarized briefly as follows. The name was proposed by Bancroft (1945 : 203) for a group of dalmanellids which differed from *Resserella* (*Resserella*) Bancroft 1928, as conceived by him, mainly in " the presence of distinct fulcral plates and supporting plates " in immature brachial valves. It can be shown, however, that the differentiation of fulcral plates was not as fundamental to the growth of the cardinalia as Bancroft maintained (Williams & Wright 1963 : 9) and in any event occurred, although less commonly, in species of *Resserella* s.s.; and since other differences given by Bancroft, like the stronger convexity of the brachial valves of *Howellites* spp., are not relevant to supra-specific classification, there was no justification for subgeneric segregation. Although Bancroft had proposed *Resserella*, he designated an assortment of shells, described by J. de C. Sowerby as *Orthis canalis*, as type species and when Schuchert & Cooper (1932 : 126) chose the lectotype they cited a specimen from the Wenlock Shale which later proved to be very close to *Orthis elegantula* Dalman, the type species of their genus *Parmorthis*. *Resserella* is therefore a synonym of *Parmorthis* but, since there is no generic difference between those Caradocian dalmanellids formerly known as " *Orthis canalis* " and given the varietal name *antiquior* by M'Coy (1852) and species of *Howellites*, *Howellites* can now be used in place of *Resserella*.

Howellites is certainly close to *Paucicrura* Cooper 1956, in many features but the invariable development of a differentially trilobed cardinal process in species assigned to the latter genus compared with the undifferentiated bilobed process of British stocks serves to distinguish between the two.

Howellites striata Bancroft
(Pl. 5, figs. 8–18)

1945 *Resserella* (*Howellites*) *striata* Bancroft : 204, pl. 26, figs. 2–10, pl. 27, figs. 13–15, pl. 28, figs. 1–3.
1945 *Resserella* (*Howellites*) *striata lineata* Bancroft : 205, pl. 26, figs. 11, 12, pl. 28, fig. 4.
1945 *Resserella* (*Howellites*) *intermedia expectata* Bancroft : 206, pl. 27, figs. 5–9, pl. 28, figs. 7, 8.

Diagnosis (emended). Subcircular, unequally biconvex *Howellites* with evenly convex sulcate brachial valve less than three-quarters as long as wide and less than one-seventh as deep as long and pedicle valve just over one-third as deep as long ; radial ornamentation finely costellate with modal count of 4 costellae per mm., 5 mm. anterior of dorsal umbo, external branching rarely occurring earlier than internal in sectors I to IV ; dental lamellae well developed, slightly divergent, less than one-quarter as long as pedicle valve, ventral muscle scar extending anteriorly for about two-fifths the length of valve and about four-fifths as wide as long in adult stages of growth ; cardinalia well defined with divergent brachiophore bases extending anteriorly for about one-fifth the length of brachial valve, and less than two-thirds as long as wide, dorsal adductor scars extending forward for about three-fifths the length of valve.

Material (Figured).	length	width (mm.)
Internal mould of pedicle valve (BB.28925)	10·0	10·0
Internal mould of brachial valve (BB.28926)	8·0	10·2
External mould of brachial valve (BB.28927)	9·0	12·0
Internal mould of brachial valve (BB.28928)	8·0	10·2
Deformed internal mould of pedicle valve (BB.28929)	8·8	8·0
External mould of brachial valve (BB.28930)	5·5	—
External mould of pedicle valve (BB.28931)	11·0	—
Internal mould of brachial valve (BB.24650)	10·5	12·0
Internal mould of pedicle valve (BB.24652)	9·5	10·0
External mould of brachial valve (BB.24650)	8·3	10·0
External mould of pedicle valve (BB.24651)	8·0	—

Horizon and localities. Allt Ddu Group : BB.28925–27 from siltstone crags in the scarp by the south side of the wall about 880 ft. east of Ty'n-y-cefn Farm, Craig y Gath (type locality of *H. striata* Bancroft 1945 : 205) ; BB.28928–31 from siltstone crags at the wall junction about 1,000 ft. east of Ty'n-y-cefn Farm, Craig

y Gath (type locality of *H. striata lineata* Bancroft 1945 : 205) ; BB.24650–52, from exposures in the gutter section on Craig y Gath, 3,400 ft. south of Glyn Mawr (type locality of *H. intermedia expectata* Bancroft 1945 : 206).

Howellites intermedia Bancroft

(Pl. 6, figs. 1–5)

1945 *Resserella* (*Howellites*) *intermedia* Bancroft : 205, pl. 27, figs. 1–4, pl. 28, figs. 5, 6.

Diagnosis (emended). Subcircular, unequally biconvex *Howellites* with evenly convex, sulcate brachial valve about three-quarters as long as wide and about one-eighth as deep as long and pedicle valve over one-third as deep as long ; radial ornamentation finely costellate with modal count of 4 costellae per mm., 5 mm. anterior of dorsal umbo, external branching rarely occurring earlier than internal in sectors I to IV ; dental lamellae well developed, slightly divergent, less than one-quarter as long as pedicle valve, ventral muscle scar extending anteriorly for just over two-fifths the length of valve and over four-fifths as wide as long in adult stages of growth ; cardinalia well defined with divergent brachiophore bases extending anteriorly for about one-fifth the length of brachial valve and just over three-fifths as long as wide, dorsal adductor scars extending forward of umbo for over one-half the length of valve.

Material (Figured).	length	width (mm.)
Internal mould of brachial valve (BB.28936)	7·0	10·2
Deformed internal mould of pedicle valve (BB.28937)	10·0	9·5
External mould of brachial valve (BB.28938)	—	9·5
External mould of brachial valve (BB.28939)	8·3	—
External mould of pedicle valve (BB.28940)	9·0	11·0

Horizon and locality. Allt Ddu Group : all specimens from siltstone crags on Craig y Gath about 120 yds. east of the ford 2,200 ft. south of Ty'n-y-Cefn (type locality 4a, 2, of *H. intermedia* Bancroft 1945 : 205).

Howellites ultima Bancroft

(Pl. 6, figs. 6–12)

1945 *Resserella* (*Howellites*) *ultima* Bancroft : 209, pl. 27, figs. 10–12, pl. 28, figs. 9, 10.

Diagnosis (emended). Subcircular, unequally biconvex *Howellites* with evenly convex, sulcate, brachial valve about three-quarters as long as wide and about one-sixth as deep as long and pedicle valve over one-third as deep as long ; radial ornamentation rather finely costellate with modal count of 4 costellae per mm., 5 mm. anterior of dorsal umbo, external branching commonly occurring earlier than internal in sectors I to IV ; dental lamellae well developed, slightly divergent, about one-quarter as long as pedicle valve, ventral muscle scar extending anteriorly for about two fifths the length of valve and over three-quarters as wide as long in

adult stages of growth ; cardinalia well-defined with divergent brachiophore bases extending anteriorly for over one-fifth the length of brachial valve and less than two-thirds as long as wide ; dorsal adductor scars extending forward of umbo for less than three-fifths the length of valve.

Material (Figured).	length	width (mm.)
Internal mould of pedicle valve (BB.28941)	9·0	10·1
Internal mould of brachial valve (BB.28942)	3·5	4·3
Internal mould of brachial valve (BB.28943)	9·0	—
Internal mould of brachial valve (BB.28944)	9·5	11·8
External mould of brachial valve (BB.28945)	4·2	5·5
External mould of brachial valve (BB.28946)	8·2	10·5
External mould of pedicle valve (BB.28947)	8·5	10·5

Horizon and locality. All specimens from siltstone exposures about 80 ft. north of the gutter on Craig y Gath (type locality of *H. ultima* Bancroft 1945 : 209).

Howellites antiquior (M'Coy)

(Pl. 6, figs. 13–19, Pl. 7, figs. 1, 2, 5, 6)

1839 *Orthis canalis* J. de C. Sowerby *in* Murchison : 640, pl. 20, fig. 8, *non* p. 630, pl. 13, fig. 12*a*.
1852 *Orthis canalis* Sowerby var. α *antiquior* M'Coy : 217.
1928*a* *Resserella canalis* (Sowerby) Bancroft : 54 pars.
1959 *Paucicrura sowerbii* Cave & Dean : 295, pl. 53, figs. 7–11.

Diagnosis (emended). Subcircular, unequally biconvex to almost plano-convex *Howellites*, brachial valve with variably defined sulcus dependent on evenness of convexity, about three-quarters as long as wide and less than one-seventh as deep as long, pedicle valve over two-fifths as deep as long ; radial ornamentation finely costellate with counts of 4 or 5 costellae per mm., 5 mm. anterior of dorsal umbo, external branching rarely occurring earlier than internal in sectors I to IV ; dental lamellae well developed, slightly divergent, less than one-quarter as long as pedicle valve, ventral muscle scar extending anteriorly for less than two-fifths the length of valve and less than four-fifths as wide as long in adult stages of growth ; cardinalia well-defined with divergent brachiophore bases extending anteriorly for about one-fifth the length of brachial valve and over one-half as long as wide, dorsal adductor scars extending forward for over one-half the length of valve.

Material (Figured).	length	width (mm.)
Internal mould of conjoined valves (ventral aspect) (BB.28948)	9·0	9·5
Deformed internal mould of pedicle valve (BB.28949)	9·5	8·5

MATERIAL (Figured) (*continued*)	length	width (mm.)
Internal mould of brachial valve (BB.28950)	8·5	11·0
Internal mould of brachial valve (BB.28951)	6·3	7·5
External mould of brachial valve (BB.28952)	8·2	11·5
External mould of brachial valve (BB.28953)	9·5	—
External mould of pedicle valve (BB.25043)	10·5	12·0
Internal mould of brachial valve (BB.28955)	10·0	—
Internal mould of pedicle valve (BB.28956)	10·0	12·3
External mould of pedicle valve (BB.28957)	10·0	—
External mould of brachial valve (BB.28958)	8·0	10·5

HORIZON AND LOCALITIES. Gelli-grîn Group : BB.28948–49, BB.28951, BB.28953 from calcareous ashes exposed above the limestone in old quarries in Ffridd Bach, south of Maes-meillion ; BB.25043 from calcareous ash crags beginning 75 ft. south of east end of ruined buildings in Ffridd Bach, south of Maes-meillion ; BB.28950, BB.28952 from calcareous ash crags 700 ft. west-north-west of BM.1338.7, south side of Bryn Pig.

The four specimens (BB.28955–58) which were collected from Lower Longvillian siltstones exposed on Gallt-yr-ancr, 440 yds. north of west from Dyffryn, one-half mile south-west of Meifod Church, the type locality for the species, have been figured for comparison with *Howellites antiquior* from the Gelli-grîn Group. Data derived from a sample composed of *Howellites* from the Lower Longvillian rocks of Gallt-yr-ancr and also of the quarry, 200 yds. east-north-east of Bwlch-y-Cibau Church (locality 38 of Whittington 1938*a* : 448), are given in Tables 43–53. The sample is indistinguishable from that consisting of the Gelli-grîn *Howellites* and the two assemblages are considered to be conspecific.

DISCUSSION. The dalmanellids found in the Allt Ddu and Gelli-grîn rocks consist mainly of sorted assemblages of *Howellites*. Bancroft (1928 : 487) listed those recovered from the Gelli-grîn Group as " *Dalmanella* (*canalis* Group) " and, as is shown in Tables 43–53, there is no significant difference in any of 11 characters between these and a sample of *Howellites antiquior* (M'Coy) from the Lower Longvillian of the Meifod District so that henceforth the Gelli-grîn shells will be referred to as *Howellites antiquior*. The Allt Ddu dalmanellids collected by Bancroft were subsequently (1945 : 204–209) allocated by him to five species and subspecies which, arranged in stratigraphical sequence, are *H. striata*, *H. striata lineata*, *H. intermedia*, *H. intermedia expectata* and *H. ultima*. Bancroft recognized

that he was contriving to classify a series of closely related stocks but he drew distinctions between them on such characters as absolute size, a meaningless difference in water sorted assemblages, the fineness of radial ornamentation and above all the earlier or later origin of internally branching costellae relative to certain external ones belonging to the same sectors. His analyses were presented in table form (Bancroft 1945 : 204) and purported to show a progressive trend in the earlier insertion of external costellae from sector I to sector IV of the brachial valves occurring at successively higher horizons. This classification suffered from two defects (Williams & Wright 1963 : 22). First, Bancroft did not subject his data to any tests of significance so that such patterns of ornamentation may not have been sufficiently different to merit the systematic recognition proferred by him. Secondly, the presentation of his data in percentage form and without hint of the actual numbers of brachial valves involved, may have inadvertently concealed the use of samples too small to be reliable and an examination of his collections, now preserved in the British Museum, in fact confirmed that they were mostly inadequate for the finely drawn discriminations he proposed. Accordingly, with the exception of *Howellites intermedia expectata*, the locality for which could not be found, larger collections of topotypic material were obtained for all the species and subspecies described by Bancroft and the data given in Tables 43–53 are based on the newer collections as well as those of Bancroft.

Table 52 shows the distribution of costellae per mm. at a standard distance of 5 mm. anterior of the umbo, for the various species assigned to *Howellites*. In every sample the modal count was 4 per mm. and although there is some variation from 3 to 6 costellae per mm. it is misleading to claim, for example, that *H. intermedia expectata* is more coarsely ribbed than *H. intermedia* (Bancroft 1945 : 208) and indeed on this character alone there is no difference between any of the six species and subspecies listed.

In an attempt to cover any possible changes in the arrangement of the radial ornamentation, 27 ribbing associations were examined for all samples. Five of these associations, essentially reflecting the proportions of internal and external branching in the first four sectors, proved to be sufficiently variable to warrant comparison by exact probability methods, and Table 53 gives the actual proportions determined for all species and subspecies as well as those of *H.* cf. *ultima* from Bancroft's locality 4b9 and of *H.* cf. *striata* from mudstones of the Lower Allt Ddu Group exposed in a field about 300 yds. north-north-east of Ty'n-y-bryn Farm where the species is associated with *Dinorthis berwynensis* (Whittington). Chi-squared tests show that neither the relatively high incidence of ī ā ī)īb̄ nor the relatively low one of ā c̄)2 a° for *H. ultima* is important but that the low proportions of 3 c̄)3 a° and 4 b̄)4 b° and the high ones for 4ā ī°)4 b̄ ī are highly significant ($p < \cdot 001$) for both *H. ultima* and *H.* cf. *ultima*. On the basis of radial ornamentation then there are only two distinct stocks—*H. ultima* (together with *H.* cf. *ultima*) and a pool of the remaining species which cannot be distinguished from one another on this character alone. Further, there are no trends leading to the predominance of external branching in any sector ; *H. ultima* is sharply dissociated from both

the younger *H. antiquior* and the older *H. intermedia expectata* and is not the climax of any gradual change.

There may, of course, have been other morphological differences resulting from changes in differential growth which had not been detected by Bancroft but which were none the less systematically important. Nine bivariate analyses, leading to estimates of growth ratios " a " or " α " and, if necessary, also inherent shape, " b " or " β ", have therefore been conducted for each of the seven samples. These covered most if not all of the morphological variations which are normally employed in taxonomy and they are set out in Tables 43–51. In all, 135 comparisons were required to discover what difference existed. Twenty-three of these could not be completed because the coefficient of correlation, r, was not significant due to the small size of one or both samples ; ten showed that significant differences ($p < \cdot 05$) existed in either the growth ratios or inherent shapes : while no differences were found in any of the remaining 102 comparisons. The most striking conclusion then, is that the samples, drawn as they were from about 1,200 ft. of mudstones and ashes, were extremely conservative in most aspects of relative growth.

Thus in the growth of the cardinalia (Tables 48, 50), analysis showed that the process was mainly a simple one with the brachiophores expanding anteriorly by about one-fifth the forward growth of the brachial valve and laterally at almost twice the rate of anterior increment. Similarly the ventral muscle field tended to expand anteriorly by less than one-half the increase in valve length (Table 49), but allometry affected some samples so that the anterior encroachment of the muscle field became accelerated in adult stages of growth. This acceleration was more obvious in the changes in the outline of the ventral scar (Table 47) because in young valves the scars tended to be slightly wider than long whereas during subsequent growth, the accelerating anterior expansion gave the average lateral encroachment as only about four-fifths the forward one. In all four attributes the variability inherent to the samples, small though it is—the coefficient of correlation is at least 0·8 for all compared samples—is sufficient to account for any shifts in the growth axis or for differences in residual shape so that no important change took place in the growth and disposition of either cardinalia or the ventral muscle field.

In the remaining five aspects of relative growth significant differences did occur. Taking the maximum length and width as indices of outline (Table 43) it can be shown that the brachial valves, although affected by allometry in some samples, tended to expand laterally about one-fifth as fast again as their anterior expansion. *H. intermedia*, however, differed from all other samples except that of *H. striata*, in a significantly faster growth in width relative to length. Now *H. striata* is much more variable than other samples of comparable size. It is indistinguishable in every respect from *H. striata lineata* which may be collected from a crag about 25 ft. above the one yielding *H. striata* and if, on the reasonable assumption that both samples represent a homogeneous morphological assemblage, these two samples are pooled, the revised growth ratio differs significantly from that of *Howellites intermedia*. The depth of the brachial valve relative to length, is difficult to measure because many of the valves collapsed during burial, which accounts for the small

size of the samples. There was also a great deal of variation during growth in that young shells tended to be much more convex than adult ones and this allometric effect is characteristic of most samples. They are all, however, comparable with an average increase in depth of about one-eighth the anterior expansion of the valve, except for *H. intermedia* which became deeper at about the same rate as *H. ultima* but was significantly more convex in its residual profile. Dorsal adductor scars are commonly deeply impressed on the valve floor even in young shells and although the anterior expansion of the muscle field relative to valve length tended to accelerate during adult stages of growth in all samples compared with *H. antiquior*, only in *H. intermedia* and *H. striata lineata* was the difference significant. The relative expansion of the adductor scar of *H. striata* was again more variable than in other

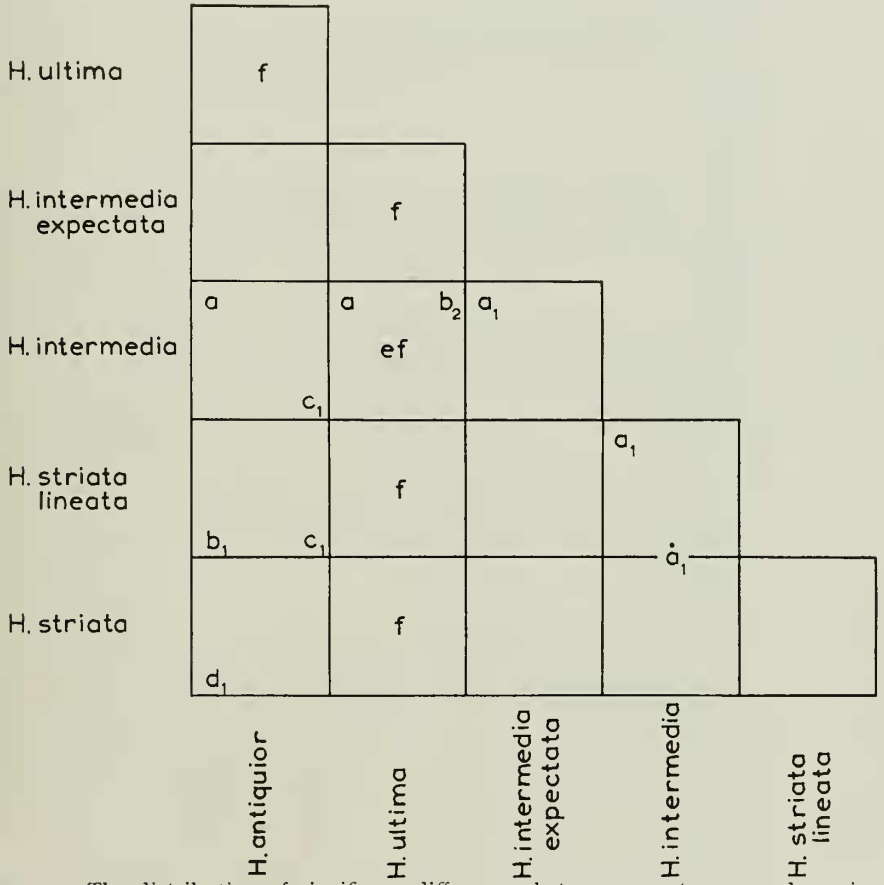

FIG. 10. The distribution of significant differences between any two named species of *Howellites* where a and b respectively represent the relative width and depth of the brachial valve, c the relative length of the dorsal adductor scars, d the relative depth of the pedicle valve, e the relative length of the dental lamellae and f the early insertion of external costellae : lower case figures 1 or 2 respectively indicate significant differences in growth rate or inherent shape.

samples but in this attribute neither the growth ratio nor the residual shape of a pooled assemblage of *H. striata* and *H. striata lineata* differed significantly from those of *H. antiquior*.

Two characters of the pedicle valve remain to be discussed. The anterior growth of the divergent dental lamellae of all samples proceeded at about one-quarter the rate of the anterior expansion of the pedicle valve, except for the dental lamellae of *H. ultima*, which grew at a sufficiently faster rate to be significantly different from the slowest expansion found among the samples, namely that of *H. intermedia*. The last feature involving changes in the profile of the pedicle valve, is probably the most interesting because it is the only one to show a progressive shift in the growth ratios from the oldest sample (that of *H. striata*) to the youngest (*H. antiquior*). The growth was mostly simple without allometric complications and involving an increase from a deepening of the valve at just over one-quarter to just under one-half the anterior expansion. The sub-carinate pedicle valves of *H. antiquior*, therefore, differ significantly from the more uniformly convex valves of *H. striata* and *H. striata lineata*, in that they deepened faster relative to length.

The implications of all these comparisons can best be summarized in diagrammatic form (Text-fig. 10). Bearing in mind that eleven characters of shell morphology have been involved in testing the homogeneity of the seven samples, the differences are really minor, yet persistent enough to suggest that some of Bancroft's species ought to be retained. *H. ultima* differs from all other assemblages in the early development of externally branching costellae in sectors III and IV ; it further differs from *H. intermedia* in the outline and profile of the brachial valve and in the relatively longer dental lamellae of the pedicle valve. *H. intermedia* may likewise be dissociated from other samples, assuming that *H. striata* and *H. lineata* belong to the same stock, in being relatively wider. It also differs from *H. antiquior* in the faster expansion of the dorsal adductor scars. In fact *H. ultima* and *H. intermedia* are so sharply distinct from other *Howellites* that one is tempted to think of them as fossil vestiges of two distinct species contemporaneous with the *H. striata-antiquior* complex and introduced briefly into the basin of deposition by changes in current direction. This assumption would explain the very close similarity between the four remaining samples. *H. antiquior* differs from both *H. striata* and *H. striata lineata* only in the greater relative depth of the pedicle valves and from the latter also in the relatively slower anterior spread of the dorsal adductor field. The *H. intermedia expectata* sample is unfortunately one affording no reliable data for the most vital attribute in this systematic procedure, namely the relative depth of the pedicle valve. In other crucial features it is clearly unrelated to *H. intermedia* but is indistinguishable from either *H. striata* s.l. or *H. antiquior* : provisionally the sample is classified with the former species.

In retrospect it is evident that Bancroft's taxonomic treatment of *Howellites* was unnecessarily discriminating. On radial ornamentation alone only *H. ultima* is distinguishable from *H. antiquior* and recourse to other, more subtle morphological changes becomes essential to preserve *H. intermedia* and *H. striata* (embracing *H. striata lineata* and *H. intermedia expectata*).

TABLE 43

	A	B	C	D	E	F	G
n	29	94	62	15	50	46	21
$\bar{l}$ mm.	6·97	4·98	5·29	6·59	5·01	5·04	4·83
(var. l)	(5·2)	(5·409)	(6·079)	(4·264)	(5·675)	(5·667)	(2·942)
$\bar{w}$ mm.	8·67	6·59	7·03	8·33	6·72	6·72	6·69
(var. w)	(6·44)	(7·714)	(8·722)	(5·536)	(9·96)	(8·553)	(5·77)
r	0·973	0·988	0·99	0·985	0·987	0·993	0·901
a	—	1·194	—	1·14	1·325	—	1·4
(var. a)	—	(0·00037)	—	(0·00297)	(0·00087)	—	(0·01942)
$\log_e \bar{l}$	1·8904	1·5069	1·5677	1·8387	1·5091	1·5167	1·5155
(var. $\log_e$ l)	(0·1014)	(0·197)	(0·1962)	(0·0938)	(0·2045)	(0·2013)	(0·1185)
$\log_e \bar{w}$	2·1183	1·8032	1·8691	2·0814	1·8052	1·8184	1·8416
(var. $\log_e$ l)	(0·0827)	(0·1648)	(0·1622)	(0·077)	(0·1997)	(0·1733)	(0·1211)
r_e	0·973	0·99	0·995	0·973	0·996	0·998	0·922
α	0·9031	0·9146	0·9092	0·906	0·9882	0·9279	1·011
(var. α)	(0·00161)	(0·00018)	(0·00014)	(0·00337)	(0·00016)	(0·00008)	(0·00807)

TABLE 43. Statistics of the length (l) and maximum width (w) of n brachial valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grîn Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).

TABLE 44

	A	B	C	D	E	F	G
n . .	16	23	24	4	16	10	9
$\bar{l}$ mm. . .	7·13	6·15	6·18	7·63	5·93	6·72	5·87
(var. l) . .	(2·241)	(4·825)	(4·943)	(3·623)	(3·753)	(3·016)	(3·39)
$\bar{th}$ mm. . .	0·76	0·94	1·03	1·3	0·72	0·96	0·9
(var. th) . .	(0·061)	(0·214)	(0·159)	(0·097)	(0·055)	(0·076)	(0·0675)
r . . .	0·758	0·841	0·82	0·53	0·825	0·665	0·545
a . .	—	—	—	—	0·121	0·1587	—
(var. a) . .	—	—	—	—	(0·00035)	(0·00176)	—
$\log_e \bar{l}$ . .	1·9428	1·7563	1·7602	—	1·7293	1·8726	—
(var. $\log_e$ l) . .	(0·043)	(0·1203)	(0·1222)	—	(0·1014)	(0·065)	—
$\log_e \bar{th}$ . .	−0·3243	−0·1703	−0·0403	—	−0·3788	−0·0803	—
(var. $\log_e$ th) . .	(0·0997)	(0·2163)	(0·1398)	—	(0·1005)	(0·0789)	—
r_e . .	0·761	0·856	0·832	—	0·854	0·682	—
α . .	1·523	1·341	1·070	—	0·9955	1·102	—
(var. α) . .	(0·0714)	(0·02288)	(0·0016)	—	(0·01917)	(0·0812)	—

TABLE 44. Statistics of the length (l) and thickness (th) of n brachial valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grîn Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).

TABLE 45

	A	B	C	D	E	F	G
n	22	27	30	6	14	18	10
$\bar{l}$ mm.	9·58	8·57	6·91	8·47	7·29	7·17	6·11
(var. l)	(1·994)	(4·067)	(9·460)	(0·668)	(13·003)	(8·883)	(7·806)
$\overline{dl}$ mm.	2·33	2·01	1·78	1·95	1·71	1·72	1·39
(var. dl)	(0·148)	(0·214)	(0·938)	(0·108)	(0·662)	(0·485)	(0·576)
r	0·771	0·933	0·775	0·687	0·957	0·942	0·874
a	0·2724	0·2293	0·3148	—	0·2256	0·2337	0·2717
(var. a)	(0·00151)	(0·00681)	(0·0014)	—	(0·00035)	(0·00038)	(0·00218)
$\log_e \bar{l}$	2·2493	2·1215	1·7789	—	1·8769	1·891	1·7151
(var. $\log_e$ l)	(0·0217)	(0·0536)	(0·2013)	—	(0·2191)	(0·1596)	(0·1895)
$\log_e \overline{dl}$	0·8326	0·6722	0·4469	—	0·4274	0·4663	0·1988
(var. $\log_e$ dl)	(0·0265)	(0·0517)	(0·2594)	—	(0·2037)	(0·1519)	(0·2610)
r_e	0·772	0·946	0·803	—	0·98	0·964	0·886
α	1·105	0·9822	1·197	—	0·9641	0·9756	1·175
(var. α)	(0·02467)	(0·00406)	(0·01819)	—	(0·00307)	(0·00421)	(0·03707)

TABLE 45. Statistics of length of pedicle valve (l) and length of dental lamellae (dl) of n pedicle valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grîn Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).

TABLE 46

	A	B	C	D	E	F	G
n . .	12	24	29	4	29	14	9
$\bar{l}$ mm. . .	9·93	7·31	7·57	8·75	5·9	7·54	5·97
(var. l) . .	(2·191)	(7·485)	(3·593)	(0·25)	(7·379)	(10·149)	(10·5)
$\bar{th}$ mm. . .	4·03	3·0	2·72	3·0	2·15	2·76	2·07
(var. th) . .	(0·819)	(1·646)	(0·516)	(1·18)	(0·844)	(1·145)	(0·828)
r . . .	0·725	0·926	0·699	0·3	0·958	0·902	0·891
a . .	0·6114	0·469	0·379	—	—	0·3359	0·2808
(var. a) . .	(0·01773)	(0·00143)	(0·00271)	—	—	(0·00175)	(0·00233)
$\log_e \bar{l}$ . .	2·2837	1·9237	1·9936	—	1·6777	1·9378	1·657
(var. $\log_e$ l) . .	(0·0217)	(0·131)	(0·0612)	—	(0·1946)	(0·1648)	(0·2586)
$\log_e \bar{th}$ . .	1·3689	1·0145	0·9667	—	0·6819	0·9448	0·64
(var. $\log_e$ th) . .	(0·0498)	(0·1681)	(0·0677)	—	(0·1672)	(0·1407)	(0·1749)
r_e . .	0·718	0·93	0·698	—	0·965	0·90	0·903
α . .	1·515	1·132	1·052	—	0·9268	0·924	0·8224
(var. α) . .	(0·1112)	(0·00788)	(0·02102)	—	(0·00219)	(0·01353)	(0·0178)

TABLE 46. Statistics of length (l) and maximum depth (th) of n pedicle valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grîn Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).

TABLE 47

	A	B	C	D	E	F	G
n . .	16	34	18	5	18	22	20
$\bar{l}$ mm. . .	3·75	3·07	2·94	3·4	3·53	3·52	3·54
(var. l) . .	(0·439)	(1·42)	(1·947)	(0·145)	(1·683)	(2·22)	(1·957)
$\bar{w}$ mm. . .	2·85	2·42	2·27	2·68	2·95	2·84	2·89
(var. w) . .	(0·162)	(0·526)	(0·796)	(0·166)	(0·769)	(0·932)	(1·0)
r . . .	0·843	0·875	0·937	−0·26	0·904	0·91	0·962
a . .	0·6076	—	—	—	—	—	—
(var. a) . .	(0·00765)	—	—	—	—	—	—
$\log_e \bar{l}$ . .	1·3068	1·0513	0·9765	—	1·198	1·1761	1·1944
(var. $\log_e$ l) . .	(0·0306)	(0·1407)	(0·2037)	—	(0·1266)	(0·1648)	(0·145)
$\log_e \bar{w}$ . .	1·0374	0·8402	0·7477	—	1·0395	0·989	1·0046
(var. $\log_e$ w) . .	(0·0198)	(0·0872)	(0·1442)	—	(0·0846)	(0·1096)	(0·1133)
r_e . .	0·845	0·884	0·926	—	0·922	0·91	0·981
α . .	0·8045	0·7873	0·8413	—	0·8174	0·8155	0·8839
(var. α) . .	(0·01323)	(0·00424)	(0·0063)	—	(0·00627)	(0·005784)	(0·00163)

TABLE 47. Statistics of length (l) and maximum width (w) of the ventral muscle scars of n pedicle valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grîn Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).

TABLE 48

	A	B	C	D	E	F	G
n. . .	61	70	42	22	56	32	19
$\bar{l}$ mm. . .	7·13	7·08	6·57	7·44	5·81	7·48	6·21
(var. l) . .	(3·794)	(6·753)	(6·16)	(2·373)	(8·733)	(4·33)	(4·286)
$\bar{c}$ mm. . .	1·47	1·49	1·47	1·45	1·28	1·6	1·41
(var. c) . .	(0·158)	(0·262)	(0·279)	(0·0766)	(0·313)	(0·184)	(0·143)
r . . .	0·897	0·932	0·934	0·824	0·97	0·94	0·98
a . .	0·2041	0·197	0·2128	0·1796	—	0·2061	—
(var. a) . .	(0·00014)	(0·00008)	(0·00014)	(0·00052)	—	(0·00017)	—
$\log_e \bar{l}$ . .	1·928	1·894	1·8157	1·9858	1·6444	1·975	1·7736
(var. $\log_e$ l) . .	(0·0725)	(0·1266)	(0·1336)	(0·0421)	(0·2303)	(0·0744)	(0·10531)
$\log_e \bar{c}$ . .	0·35	0·3431	0·3247	0·3534	0·1594	0·4357	0·3097
(var. $\log_e \bar{c}$) . .	(0·0706)	(0·1114)	(0·1211)	(0·0363)	(0·1749)	(0·0686)	(0·0677)
r_e . .	0·895	0·936	0·939	0·831	0·982	0·962	0·993
α. . .	0·9868	0·938	0·952	0·9285	0·8714	0·9602	0·8018
(var. α) . .	(0·0033)	(0·0016)	(0·00269)	(0·01334)	(0·0005)	(0·00229)	(0·00529)

TABLE 48. Statistics of length of brachial valve (l) and length of cardinalia (c) of n brachial valves of *Howellites antiquior* (M'Coy.) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grîn Group, Bala (B) *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).

TABLE 49

	A	B	C	D	E	F	G
n . .	23	40	30	7	17	19	11
$\bar{l}$ mm. . .	9·51	8·2	7·46	8·26	7·91	6·97	7·55
(var. l) . .	(2·012)	(8·252)	(7·065)	(1·253)	(9·606)	(9·203)	(5·846)
$\bar{sc}$ mm. . .	3·61	3·1	3·04	3·23	3·33	3·13	2·93
(var. sc) . .	(0·404)	(1·535)	(1·414)	(0·58)	(1·894)	(2·311)	(1·129)
r . . .	0·808	0·944	0·976	0·806	0·979	0·984	0·985
a . .	0·4481	—	—	0·6804	0·444	0·5011	0·4393
(var. a) . .	(0·00332)	—	—	(0·03245)	(0·00055)	(0·00047)	(0·000641)
$\log_e \bar{l}$ . .	2·2413	2·0455	1·9499	2·1021	1·9948	1·8549	1·973
(var. $\log_e$ l) . .	(0·0217)	(0·1159)	(0·1194)	(0·0185)	(0·1442)	(0·1733)	(0·097)
$\log_e \bar{sc}$ . .	1·2681	1·0572	1·0407	1·1452	1·124	1·0351	1·013
(var. $\log_e$ sc) .	(0·0306)	(0·1484)	(0·1424)	(0·0545)	(0·1579)	(0·2118)	(0·1239)
r_e . .	0·806	0·945	0·991	0·835	0·967	0·995	0·985
α . .	1·187	1·131	1·092	1·717	1·046	1·106	1·13
(var. α) . .	(0·00332)	(0·00361)	(0·00076)	(0·1784)	(0·00474)	(0·00719)	(0·0041)

TABLE 49. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) of n pedicle valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grîn Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).

TABLE 50

	A	B	C	D	E	F	G
n . .	53	57	26	9	31	15	13
$\bar{l}$ mm. . .	1·46	1·51	1·5	1·48	1·25	1·65	1·37
(var. l) . .	(0·14)	(0·266)	(0·25)	(0·076)	(0·385)	(0·142)	(0·139)
$\bar{w}$ mm. . .	2·49	2·78	2·41	2·7	2·03	2·83	2·18
(var. w) . .	(0·434)	(0·958)	(0·69)	(0·385)	(1·193)	(0·5493)	(0·54)
r . . .	0·849	0·939	0·953	0·621	0·959	0·906	0·845
a . . .	1·761	1·898	1·661	2·246	1·761	1·967	1·969
(var. a) . .	(0·01697)	(0·00775)	(0·00106)	(0·44298)	(0·00858)	(0·05326)	(0·08806)
$\log_e \bar{l}$ . .	0·3431	0·3568	0·3528	0·3748	0·1131	0·4754	0·279
(var. $\log_e$ l) . .	(0·064)	(0·1105)	(0·1053)	(0·0344)	(0·2199)	(0·0507)	(0·0715)
$\log_e \bar{w}$ . .	0·8793	0·9641	0·8235	0·9674	0·5809	1·0068	0·7253
(var. $\log_e$ w) . .	(0·0667)	(0·1168)	(0·1122)	(0·0517)	(0·2541)	(0·0669)	(0·1079)
r_e . .	0·863	0·939	0·96	0·628	0·974	0·903	0·857
α . .	1·021	1·028	1·033	1·226	1·075	1·149	1·229
(var. α) . .	(0·00521)	(0·00227)	(0·00348)	(0·13)	(0·00205)	(0·01874)	(0·03637)

TABLE 50. Statistics of length (l) and maximum width (w) of cardinalia of n brachial valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grîn Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).

TABLE 51

	A	B	C	D	E	F	G
n	62	68	31	22	40	32	17
$\bar{l}$ mm.	7·39	7·28	6·94	7·43	7·23	7·61	6·33
(var. l)	(3·148)	(6·131)	(4·633)	(2·42)	(5·542)	(4·408)	(4·879)
$\overline{ad}$ mm.	4·09	3·95	3·92	3·95	3·93	4·14	3·73
(var. ad)	(0·877)	(1·617)	(1·544)	(0·756)	(2·252)	(1·533)	(1·511)
r	0·94	0·966	0·985	0·946	0·873	0·963	0·944
a	0·5279	0·5135	0·5774	0·5589	—	—	0·5565
(var. a)	(0·00054)	(0·00027)	(0·000343)	(0·00164)	—	—	(0·00225)
$\log_e \bar{l}$	1·9719	1·9303	1·8913	1·984	1·928	1·9928	1·8341
(var. $\log_e$ l)	(0·0564)	(0·1096)	(0·0919)	(0·043)	(0·1005)	(0·0734)	(0·115)
$\log_e \overline{ad}$	1·3831	1·3243	1·318	1·3503	1·3005	1·3779	1·2642
(var. $\log_e$ ad)	(0·0507)	(0·0988)	(0·0962)	(0·0468)	(0·1362)	(0·0856)	(0·1044)
r_e	0·948	0·966	0·987	0·959	0·881	0·98	0·946
α	0·9481	0·9495	1·023	1·043	1·164	1·08	0·9528
(var. α)	(0·00152)	(0·00092)	(0·00093)	(0·00437)	(0·00799)	(0·00154)	(0·00683)

TABLE 51. Statistics of length of brachial valve (l) and length of adductor scar from umbo (ad) of n brachial valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grîn Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).

	costellae per mm.				
	2	3	4	5	6
H. antiquior (M'Coy) from Meifod	—	—	8	3	1
H. antiquior (M'Coy) from Bala	—	—	16	13	1
H. ultima Bancroft	—	3	23	8	—
H. intermedia expectata Bancroft	—	1	7	—	—
H. intermedia Bancroft	—	—	14	7	2
H. striata lineata Bancroft	—	—	12	8	—
H. striata Bancroft	—	—	8	3	1

TABLE 52. The distribution of brachial valves of given species of *Howellites* with 2–6 costellae per mm., 5 mm. antero-medianly of the dorsal umbones.

TABLE 53

	1 ā1̄)1 b̄	2 c̄)2 a°	3 c̄)3 a°	4 b̄)4 b°	4 ā 1°)4 b̄1̄
H. antiquior (M'Coy)—Meifod	5/7	1/1	9/10	10/11	0/2 (1)
H. antiquior (M'Coy)—Bala	4/16	9/9	30/32 (2)	21/22 (4)	2/12
H. ultima Bancroft . .	11/24 (2)	13/20	19/67 (4)	29/64 (13)	17/23 (2)
H. cf. *ultima* Bancroft . .	2/9 (1)	0/5	11/45 (2)	27/44 (6)	11/12 (1)
H. intermedia expectata Bancroft	0/1	0/2	6/8 (2)	7/10 (1)	0/5
H. intermedia Bancroft . .	7/40 (7)	25/33	49/68	38/48 (4)	1/23 (1)
H. striata lineata Bancroft .	4/14 (3)	8/10	27/36	25/31 (4)	1/13 (2)
H. striata Bancroft . .	1/10 (2)	6/8	23/32 (2)	16/23 (6)	3/11 (2)
H. cf. *striata* Bancroft . .	4/10 (2)	4/5	21/28 (1)	13/19 (7)	1/11 (1)

TABLE 53. Proportions of brachial valves of given species of *Howellites* showing the earlier insertion of 5 costellae relative to 5 others (with the number of valves in which both costellae originated at the same growth stage in brackets).

Genus ***ONNIELLA*** Bancroft 1928*a*

DIAGNOSIS (emended). Subcircular, gently and unequally biconvex dalmanellids with pedicle valve more deeply convex than sulcate brachial valve and evenly convex to subcarinate in transverse profile ; radial ornamentation fascicostellate to multicostellate with externally branching costellae common in first four sectors of brachial valve ; ventral interarea, short, curved, apsacline with open delthyrium and small umbo ; dorsal interarea, short and curved, anacline, notothyrium commonly filled by cardinal process ; shell punctate.

Ventral interior with strong or massive teeth supported by divergent dental lamellae, pedicle callist well developed, muscle field subpentagonal to widely cordate in outline with submedian diductor lobes extending beyond dental lamellae but rarely enclosing a narrow, lanceolate adductor scar ; ventral pallial sinus pattern lemniscate with narrowly divergent *vascula media* branching well posterior of commissure.

Dorsal interior with undifferentiated bilobed cardinal process, commonly expanded into semi-ovoid structure, brachiophores with their bases greatly divergent relative to their tops, fulcral plates rarely developed ; dorsal adductor scars elongate with posterior elements either smaller than or about equal to anterior ones ; pallial sinus pattern not well known, probably lemniscate.

Type species. *Onniella broeggeri* Bancroft.

Discussion. Bancroft (1928*a* : 55–57, 63–68) erected this genus with the intention of recognizing the characteristic profile of the shell and the degree of external branching in the first four sectors of the radial ornamentation on the brachial valve. Three new species were assigned to the genus, *O. broeggeri*, *O. reuschi* and *O. avelinei* and it is evident from his discussion of the last species (p. 57) that he considered it to be different from *O. broeggeri* only in details of outline and profile. Bancroft (1945 : 209–211) however, proposed another genus, *Soudleyella*, to embrace the type species, *S. soudleyensis* Bancroft and also *O. avelinei*. In his discussion of *Soudleyella* he made no direct comparison with *Onniella* although later (p. 215) he did remark that *Onniella* is " a large *Soudleyella*-like genus with a small ventral umbo, a large and complex cardinal process, widely divergent socket lines and a large anterior and small posterior scars in the dorsal valve ". But a small ventral umbo and widely divergent brachiophore bases (see Williams & Wright 1963 : 29) are also typical of *Soudleyella* while a complex cardinal process, which is known in gerontic shells of *Soudleyella*, is not invariably developed in species of *Onniella* and even Bancroft (1945 : 215) refers to " abnormal *Onniella* " with subequal adductor scars. In fact the two genera are inseparable morphologically and judging from textual emphasis on chronology, the real reason for Bancroft's reappraisal of his earlier systematic studies was probably the stratigraphical discontinuity between the species he assigned to *Soudleyella*, which were Harnagian and Soudleyan in age, and those he restricted to *Onniella* which ranged through the Marshbrookian, Actonian and Onnian. This use of time as a factor in taxonomic practice is a dangerous one. It ignores the effects of facies shifts, sorting of death assemblages and other controls governing the distribution of fossil remains and is not, at least for the present, a worthy substitute for morphological comparison.

Onniella ostentata sp. nov.

(Pl. 7, figs. 3, 4, 7–11, 16)

Diagnosis. Subcircular to subquadrate unequally biconvex *Onniella* with sulcate brachial valve about three-quarters as long as wide and about one-seventh as deep as long and evenly convex pedicle valve over one-quarter as deep as long ; radial ornamentation rather coarsely fascicostellate with modal count of 3 costellae per mm., 5 mm. anterior of dorsal umbo, external branching freely developed in sectors I to IV ; dental lamellae divergent, short, less than one-quarter as long as pedicle valve, teeth massive, crenulated ; adult ventral muscle field subpentagonal, less than two-fifths as long as pedicle valve and over four-fifths as wide as long with

submedian diductor lobes extending beyond but not enclosing lanceolate adductor scar ; cardinalia massive, less than one-fifth as long as brachial valve and less than one-half as long as wide, consisting of thick cardinal process commonly bilobed and filling entire notothyrium even in young growth stages and divergent brachiophores so exaggerated by secondary shell deposition in adult shells as to form a solid transverse bar ankylosed with thickened median ridge, adductor scars, subquadrate with posterior and anterior elements subequal, divided by the median ridge and extending forward for over one-half the length of brachial valve.

		length	width (mm.)
Holotype.	Internal mould of brachial valve (BB.29030)	7·0	8·5
Paratypes.	External and internal mould of brachial valve (BB.28932–33)	10·0	—
	Internal mould of brachial valve (BB.28866)	—	4·7
	Internal and external mould of brachial valve (BB.28868–69)	8·0	9·5
	External mould of brachial valve (BB.28867)	8·0	10·0
	Internal mould of pedicle valve (BB.28870)	8·2	—
	External mould of pedicle valve (BB.28871)	9·5	—

Horizon and localities. Gelli-grîn Group : BB.29030, BB.28870–71 from calcareous ash crags about 75 ft. south of the east end of ruined buildings in Ffridd Bach, south of Maes-meillion ; BB.28932–33, BB.28866 from calcareous ashes along the east side of the southern Rhiwlas Limestone outlier on Creigiau Bychain ; BB.28868–69 from calcareous ashes exposed at south end of wood, 850 ft. west of Gelli-grîn Farm ; BB.28867 from calcareous ashes exposed south of track, 1,900 ft. east-north-east of Bryn-briglas Farm.

Onniella cf. *soudleyensis* (Bancroft)

(Pl. 7, figs. 12–15, 17, 18)

Description. Subcircular, unequally biconvex *Onniella* with a sulcate brachial valve about three-quarters as long as wide and about one-seventh as deep as long and subcarinate pedicle valve less than one-third as deep as long ; radial ornamentation fascicostellate with about 4 costellae per mm., 5 mm. anterior of the dorsal umbo ; external branching freely developed in sectors I to IV ; teeth strong, dental lamellae divergent, short just over one-fifth as long as the pedicle valve, ventral muscle field subpentagonal in adult valves extending anteriorly for less than two-fifths the length of the valve and over two-thirds as wide as long with the submedian diductor lobes extending forward of, but not enclosing, the lanceolate

adductor scar ; cardinal process strong, bilobed and crenulated posteriorly in adult valves but also thickening into a trilobed structure, brachiophores, strong, divergent, rarely flanked by fulcral plates, extending anteriorly for less than one-quarter the length of the brachial valve and over three-fifths as long as wide, dorsal adductor scars oval with anterior elements slightly larger than posterior ones, divided by a median ridge and extending anteriorly for nearly three-fifths the length of the brachial valve.

Material (Figured).	length	width (mm.)
Internal mould of brachial valve (BB.28874)	9·5	11·0
Internal mould of brachial valve (BB.28873)	3·0	3·8
Internal mould of pedicle valve (BB.28872)	9·0	9·5
External mould of pedicle valve (BB.28875)	7·5	8·5
External mould of brachial valve (BB.28876)	11·2	12·5
External mould of brachial valve (BB.28877)	3·5	5·0

Horizon and locality. Nant Hir Group : all specimens from mudstones exposed in left bank of Nant Hir, 600 ft. north-east of Cefn-y-maes Farm.

Discussion. Two distinct forms of *Onniella* occurred in the Caradocian rocks of the Bala district, one from the Nant Hir Group, which compares with the description given by Bancroft (1945 : 210) for *S. soudleyensis* and may, provisionally at least, be referred to that species, and another from the Gelli-grîn Group which is new.

Both stocks are alike in a number of attributes, including the outline of the brachial valve, the relative length of the dorsal adductor scars, the relative depth of the pedicle valve, and the relative lengths of the dental lamellae and the ventral muscle scar (Tables 55, 59, 60, 61, 63). Few data were obtained for some characters of *S. soudleyensis* but the mean percentage depth relative to length of six brachial valves was 15·3% (variance 7·25) which is not importantly different from the mean depth of the brachial valves of *O. ostentata* ; and although the mean percentage width relative to length of two ventral muscle scars, at 70, was 13 less than that for the muscle scars of *O. ostentata* (Table 62) larger samples of *S. soudleyensis* may show the difference to be insignificant. Similarly, although the small sample of ribbing associations in *S. soudleyensis* shows that the pattern is the same as that of *O. ostentata*, it is significantly finer ($p < ·01$). 2, 3, 4 and 5 costellae per mm. were counted 2 and 5 mm. respectively antero-medianly of the dorsal umbones of 0, 2, 10, 3 and 1, 11, 3, 0 brachial valves of *O. ostentata*. Only two specimens of *S. soudleyensis* were sufficiently well preserved to give counts at the 5 mm. growth stage ; both were of 4 costellae per mm. At 2 mm., 4, 5, 6 and 7 costellae per mm. were noted in 1, 13, 3 and 3 specimens respectively.

But perhaps the most obvious difference ($p < \cdot 01$) is in the development of the cardinalia which were consistently shorter relative to the length of the brachial valve and consistently wider relative to their own length in *O. ostentata*. These discrepancies resulted from the extravagant deposition of secondary shell substance around the brachiophores and cardinal process of *O. ostentata*, which was not simply a gerontic secretion as is shown by comparing the development of the cardinal process. In *S. soudleyensis*, the shaft, with or without a small posterior node representing the myophore, was exclusively characteristic of all growth stages of brachial valves up to 2 mm. long and occurred in 1 out of 5 valves between 3 and 4 mm. long. An enlarged bilobed myophore with a crenulated posterior face first appeared in 4 out of 11 valves 2 to 3 mm. long and persisted even in a valve 8 mm. long while a cardinal process, which was so enlarged that both myophore and shaft were entirely buried in secondary shell, did not occur in any valve less than 4·5 mm. long. In contrast, in the four youngest valves recovered of *O. ostentata*, which were all between 3–4 mm. long, the cardinal process was already a massive, semi-ovoid structure and the brachiophores cemented together to form a transverse bar.

TABLE 54

	A	B	C
1 b̄) 1 ā°	2/6 (1)	—	1/3
2 b̄) 2 ā°	18/19 (1)	4/4	3/3
2 ā ī) 2 b̄	2/15 (2)	7/8 (1)	1/1
3 ā ī ā) 3 a°	1/18	4/14	1/7
3 ā ī ā) 2 a°	1/3	9/9	1/1
3 c̄) 3 a°	1/18	1/14	1/7
3 ā 1°) 3 b̄ ī	1/3	2/5	—
4 b̄) 4 b°	0/12	1/17	0/2

TABLE 54. The proportions of the earlier insertion of 8 costellae relative to 8 others (with the number of valves in which both costellae originated at the same growth stage in brackets) for samples of *Onniella ostentata* sp. nov. (A), *O. broeggeri* Bancroft (B) and *O.* cf. *soudleyensis* (Bancroft) (C).

TABLE 55

	A	B
l̄ mm. (var. l)	4·76 (4·169)	3·44 (6·566)
w̄ mm. (var. w)	6·34 (5·538)	4·66 (7·691)
r	0·977	0·99
a (var. a)	1·152 (0·00163)	1·082 (0·00061)

TABLE 55. Statistics of length (l) and maximum width (w) of 39 brachial valves of *Onniella ostentata* sp. nov. (A) and of 40 brachial valves of *O.* cf. *soudleyensis* (Bancroft) (B).

TABLE 56

l mm. (var. l) . .	6·28	(2·426)
$\overline{th}$ mm. (var. th) . .	0·96	(0·116)
r . . .	0·467	
a (var. a) . . .	0·2186	(0·00235)

TABLE 56. Statistics of length (l) and depth (th) of 18 brachial valves of *Onniella ostentata* sp. nov.

TABLE 57

	A		B	
$\bar{l}$ mm. (var. l) . .	7·3	(1·998)	3·04	(2·766)
$\bar{c}$ mm. (var. c) . .	1·34	(0·082)	0·7	(0·095)
r . . .	0·881		0·945	
a (var. a) . . .	0·2026	(0·00036)	0·1852	(0·0001)

TABLE 57. Statistics of length of brachial valve (l) and length of cardinalia (c) of 28 specimens of *Onniella ostentata* sp. nov. (A) and 39 of *O.* cf. *soudleyensis* (Bancroft) (B).

TABLE 58

	A		B	
$\bar{l}$ mm. (var. l) . .	1·31	(0·099)	0·77	(0·141)
$\bar{w}$ mm. (var. w) . .	2·78	(0·45)	1·26	(0·367)
r . . .	0·776		0·958	
a (var. a) . . .	2·132	(0·07861)	1·6134	(0·00738)

TABLE 58. Statistics of length (l) and maximum width (w) of the cardinalia of 25 brachial valves of *Onniella ostentata* sp. nov. (A) and of 31 brachial valves of *O.* cf. *soudleyensis* (Bancroft) (B).

TABLE 59

	A		B	
$\bar{l}$ mm. (var. l) . .	7·42	(1·285)	3·72	(4·878)
$\overline{ad}$ mm. (var. ad) . .	3·88	(0·506)	2·14	(1·04)
r . . .	0·813		0·884	
a (var. a) . . .	0·6275	(0·00607)	0·4617	(0·00258)

TABLE 59. Statistics of length of brachial valve (l) and length of adductor scar from the umbo (ad) of 24 specimens of *Onniella ostentata* sp. nov. (A) and of 20 specimens of *O.* cf. *soudleyensis* (Bancroft) (B).

TABLE 60

	A		B	
$\bar{l}$ mm. (var. l) . .	8·08	(5·349)	4·7	(6·898)
$\overline{th}$ mm. (var. th) . .	2·18	(0·378)	1·45	(0·644)
r . . .	0·72		0·965	
a (var. a) . . .	0·2658	(0·00308)	0·3056	(0·00043)

TABLE 60. Statistics of length (l) and depth (th) of 13 pedicle valves of *Onniella ostentata* sp. nov. (A) and of 17 pedicle valves of *O.* cf. *soudleyensis* (Bancroft) (B).

TABLE 61

	A		B	
l̄ mm. (var. l)	7·94	(6·051)	5·99	(7·288)
s̄c̄ mm. (var. sc)	2·94	(1.304)	2·23	(1·122)
r	0·9		0·966	
a (var. a)	0·4642	(0·00274)	0·3924	(0·00206)

TABLE 61. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) of 17 specimens of *Onniella ostentata* sp. nov. (A) and of 7 specimens of *O.* cf. *soudleyensis* (Bancroft) (B).

TABLE 62

l̄ mm. (var. l)	2·88	(1·194)
w̄ mm. (var. w)	2·43	(0·458)
r	0·912	
a (var. a)	0·6194	(0·00587)

TABLE 62. Statistics of length (l) and maximum width (w) of ventral muscle scar of 13 specimens of *Onniella ostentata* sp. nov.

TABLE 63

	A		B	
l̄ mm. (var. l)	7·3	(3·155)	4·48	(5.835)
d̄l mm. (var. dl)	1·74	(0·212)	0·98	(0·29)
r	0·968		0·971	
a (var. a)	0·2592	(0·00038)	0·2229	(0·00021)

TABLE 63. Statistics of length of pedicle valve (l) and length of dental lamellae (dl) of 13 specimens of *Onniella ostentata* sp. nov. (A) and of 16 specimens of *O.* cf. *soudleyensis* (Bancroft) (B).

The massively developed cardinalia of *O. ostentata* distinguish it from the other species of *Onniella* described by Bancroft. In other characters it resembles *O. broeggeri* Bancroft but as can be seen from Table 54 the Gelli-grîn shells also differed significantly ($p < \cdot 01$) at least in the relatively early insertion of the costella 2 b̄.

Genus ***BANCROFTINA*** Sinclair 1946

TYPE SPECIES. *Raymondella typa* Whittington by original designation of Sinclair (1946 : 295).

Bancroftina sp.

(Pl. 7, figs. 19–23)

DESCRIPTION. Subcircular, unequally biconvex *Bancroftina* with a shield-shaped, gently convex, shallowly sulcate brachial valve about four-fifths as long as wide and a deeply and evenly convex pedicle valve, over two-fifths as deep as long with a short, curved, apsacline interarea ; radial ornamentation costellate with 2 or 3 costellae per mm. at 10 mm. antero-medianly of the dorsal umbo, external branching rare ; ventral muscle scar bilobate, slightly longer than wide and extending forward for less than one-third the length of the valve ; cardinal process massive, fissured

and united with a strong high median ridge extending anteriorly for over half the length of the brachial valve and separating a pair of elongate adductor scars, brachiophores widely divergent, subtriangular in outline, sockets narrow, oblique.

Material (Figured).	length	width (mm.)
External mould of pedicle valve (BB.29124)	—	—
Incomplete external moulds of conjoined valves (BB.29148)	17·0	—
Internal mould of brachial valve (BB.29149)	17·0	17·0
External and internal moulds of conjoined valves (BB.29146–47)	16·0	16·5

Horizon and locality. Gelli-grîn Group : all specimens from the calcareous ashes above the Gelli-grîn Limestone in the old quarries 1,800 ft. south of Bryn-melyn Farm.

Discussion. Rare moulds of *Bancroftina* are known from the top calcareous ashes of the Gelli-grîn Group and have been compared by Bancroft (1945 : 201) with *B. robusta*. The similarities, however, may prove not to be important because, although the outline of the ventral muscle field is like that of *B. robusta*, the radial ornamentation with the early insertion of 2ā is more reminiscent of *B. typa* (Whittington) (see Bancroft 1945 : 198). In fact the differences between *B. typa* and *B. robusta*, like the larger size, the absence of " growth lines " and the shallow brachial valve etc. of the latter, are not necessarily significant and until comparative studies of these Shropshire forms together with larger collections of the Bala stock have been made, it would be misleading to attempt a specific identification of the Welsh specimens.

Family HARKNESSELLIDAE Bancroft 1928*b*

Genus ***REUSCHELLA*** Bancroft 1928*b*

Type species. *Reuschella semiglobata* Bancroft by original designation of Bancroft (1928*b* : 180).

Reuschella* cf. *horderleyensis Bancroft

(Pl. 8, figs. 1–10)

Description. Shell typically transversely subrectangular in outline but commonly modified by the early development of a pair of ears at the hinge-line so that the postero-lateral angles are acute, with relatively faster growth anterior of the hinge-line the postero-lateral angles become obtuse especially in adult shells, brachial valve about seven-tenths as long as wide, strongly and evenly convex on either side of the deep, angular median sulcus and about one-third as deep as long, but tending to flatten out laterally, pedicle valve unevenly convex, less than one-third as deep as long at the sharply angular median fold which, in adult valves, is flanked by a pair of shallow sulci passing laterally into a pair of shallow folds ; radial ornamentation fascicostellate with a modal count of 3 costellae per mm. in the

second sector, 10 mm. anterior of the dorsal umbo, externally branching costellae freely arising in sectors III and IV ; dental lamellae narrowly divergent, thin, extending forward for about one-fifth the length of the pedicle valve, teeth ridge-like, oblique to hinge-line ; pedicle callist small, ventral muscle field subtriangular to bilobed about four-fifths as wide as long with the submedian diductor lobes extending forward for over one-third the length of the pedicle valve but not enclosing the wide median adductor ; ventral pallial sinus pattern probably inequidistributate saccate; crenulated myophore and shaft of adult brachial valves fused into elongately semi-oval structure commonly buttressed by low, ancillary struts, sockets, long, divergent and defined by fulcral plates extending laterally for just under twice the length of the narrowly divergent brachiophore bases which extend forward for about one-sixth the length of the brachial valve, crural pits small ; adductor pits deep with the anterior boundaries to the scars reaching forward of the dorsal umbo for less than one-half the length of the brachial valve ; dorsal pallial sinus pattern probably inequidistributate saccate.

Material (Figured).	length	width (mm.)
Internal mould of conjoined valves (BB.29132)	22·0	—
Internal and external moulds of brachial valve (BB.28968–69)	7·0	10·2
Internal mould of pedicle valve (BB.28970)	4·2	7·0
Internal mould of brachial valve (BB.28971)	17·0	23·0
External mould of brachial valve (BB.28972)	—	—
Internal mould of pedicle valve (BB.28973)	16·5	20·5
Internal mould of brachial valve (BB.28974)	16·0	21·0
External mould of pedicle valve (BB.28975)	—	—

Horizon and locality. Allt Ddu Group : all specimens from mudstones exposed on the western slopes of Coed Mawr, 1,200 ft. west-north-west of Rhiwlas House.

Reuschella horderleyensis Bancroft *undulata* subsp. nov.
(Pl. 8, figs. 11–17)

Diagnosis. Shell typically transversely subrectangular in outline but commonly modified by early development of ears at hinge line, acute postero-lateral angles later transformed to obtuse ones by faster growth of lateral commissure, brachial valve just over two-thirds as long as wide and evenly convex on either side of deep, angular median sulcus and over one-quarter as deep as long but tending to flatten laterally, pedicle valve over one-third as deep as long at sharply angular median fold, flanking submedian rounded sulci and complementary lateral folds well

developed ; radial ornamentation fascicostellate with modal count of 3 costellae per mm. in second sector, 10 mm. anterior of dorsal umbo, externally branching costellae freely arising in Sectors III and IV ; dental lamellae divergent, then, extending forward for about one-fifth of the length of pedicle valve, teeth strong, obliquely disposed to hinge line ; pedicle callist small, ventral muscle field subpentagonal to bilobed about four-fifths as wide as long with submedian diductor lobes extending forward for about one-third the length of pedicle valve but not enclosing wide, median adductor scar ; crenulated myophore and shaft of adult brachial valves fused into massive semi-oval to semi-circular structure, sockets long, divergent and defined by fulcral plates extending laterally for over one-half as much again as the length of narrowly divergent brachiophore bases which extend forward for about one-fifth the length of brachial valve, crural pits small ; adductor pits deep, anterior boundaries to adductor scars, poorly defined, reaching forward of dorsal umbo for about two-fifths the length of brachial valve.

		length	width (mm.)
Holotype.	Internal mould of pedicle valve (BB.28860)	16·0	21·0
Paratypes.	External and internal moulds of brachial valve (BB.28861–62)	12·0	—
	External mould of pedicle valve (BB.29031)	17·0	—
	External mould of pedicle valve (BB.28863)	21·0	29·0
	Internal mould of brachial valve (BB.28864)	—	—
	Internal mould of brachial valve (BB.28865)	—	—

Horizon and localities. Gelli-grîn Group : BB.28860 from calcareous ashes exposed south of track, 1,900 ft. north-east of Bryn-briglas Farm ; BB.28861–62, BB.28865 from calcareous ash crags 40 ft. south of west end of ruined building in Ffridd Bach, south of Maes-meillion ; BB.29031 from calcareous ashes immediately west of fence at south-east end of prominent scarp of Rhiwlas Limestone, 500 ft. south-west of BM.1338.7, Bryn Pig ; BB.28863 from calcareous ashes above limestone in quarries east of fence, 650 ft. west-north-west of BM.1407.6, Bryn Pig ; BB.28864 from ashy mudstones in right bank of the Hirnant, 1,200 ft. east-north-east of Ty'n-y-wern Farm.

Discussion. Anglo-Welsh species of *Reuschella* were segregated by Bancroft (1945 : 239) into two distinct groups typified by *R. bilobata* (J. de C. Sowerby) and *R. horderleyensis* Bancroft. The distinction between them was finely drawn, resting on the concave profile and independent lateral folds of the pedicle valve of the *R. bilobata* group and especially on the late insertion of costella 2a° in the brachial valves of the *R. horderleyensis* group. These differences are not taxonomically decisive because the Bala *Reuschella* are akin to *R. horderleyensis* in the pattern of radial ornamentation (Table 64), but also display variably developed lateral

folds as indeed do specimens of *R. horderleyensis* from the Llanyblodwel Beds (Whittington 1938*a* : 450) and even some shells of the closely related *R. oblonga* (Whittington 1938 : 252). This contradiction suggests that only ribbing can be effectively employed to distinguish between the two groups and that those Bala shells from the highest Allt Ddu mudstones and Gelli-grîn ashes, which possess well developed lateral folds, are more appropriately compared with *R. horderleyensis* than *R. bilobata*.

The sample of *R. horderleyensis* obtained from the Llanyblodwel Beds was too small to use for comparisons of growth but in every respect of proportion for the characters listed in Tables 65–73 it did not differ from the older *Reuschella* found in the Bala district which may therefore be described, provisionally at least, as conspecific. The specimens making up this Bala sample were recovered from Lower Allt Ddu rocks where they are associated with *Dinorthis berwynensis* (Whittington) and *Heterorthis retrorsistria* (M'Coy). A few moulds, also comparable with *R.* cf. *horderleyensis* occur sporadically in the middle part of the Allt Ddu Group but the genus becomes quite common again in the highest Allt Ddu and the succeeding Gelli-grîn Group, and when these specimens were compared with the older sample they were found to differ sufficiently to constitute a new subspecies.

Data essential to the comparison of the new subspecies with the older *Reuschella* cf. *horderleyensis* are set out in Tables 64–73. Only small numbers of brachial valves were well enough preserved to show details of radial ornamentation but it is evident that there is no difference between the two samples and the texture is also similar ; 2 and 3 costellae per mm. were counted at a distance of 10 mm. anterior of the umbones of 3 and 7 brachial valves of *R.* cf. *horderleyensis* and 3 and 7 of the new subspecies respectively. Using length, width and depth for quantitative estimates of both the growth and residual proportions of shell outline and profile (Tables 65, 66) it was found that in such attributes the samples were alike, as they were too in the development of the lateral folds in the pedicle valves although those of the subspecies are better defined.

Internally, also, the samples were mainly so alike that they could have been drawn from the same population. The anterior boundary to the dorsal adductor field is commonly impressed in *Reuschella* cf. *horderleyensis* ; it moved forward of the dorsal umbo at slightly less than one-half the increase in length of the brachial valve (Table 69). Such impressions were found in only two valves of the new subspecies but they were similarly proportioned. In both samples the anterior expansion of the dental lamellae (Table 73) and the relative width of the ventral muscle scar (Table 72) increased at a comparable rate and at the same time retained similar residual proportions ; but in respect of the forward migration of the ventral muscle scars relative to the length of the pedicle valves, that of *R.* cf. *horderleyensis* was significantly faster ($\cdot 05 > p > \cdot 02$). Moreover, although the lateral growth of the fulcral plates did not differ significantly (Table 68) the brachiophore bases of the new subspecies were inherently larger than those of *R.* cf. *horderleyensis* but extended anteriorly relative to the length of the brachial valve at a significantly slower rate ($\cdot 05 > p > \cdot 02$). These statistics show that the cardinalia of younger

members of the *R. horderleyensis* " group " underwent an anterior shortening relative to their width in a manner recalling the increasing convergence of the " pre-socket lines " reported by Bancroft (1928 : 181) for the *R. bilobata* " group ".

Reuschella, recovered from the highest Allt Ddu and succeeding Gelli-grîn Groups, thus differs from *R. horderleyensis* in the relatively faster anterior expansion of both the supporting bases to the brachiophores and the ventral muscle field, which differences are worthy of subspecific recognition.

TABLE 64

	A	B
2 ā ī 2 a°	10/10	16/16
2 b̄) 2 a°	8/8	15/15
2 b̄ ī) 2 a°	1/1	6/6
2 c̄) 2 a°	2/2	8/8
3 ā ī) 3 a°	1/7 (4)	4/11 (1)
3 b̄) 3 a°	1/11 (1)	2/7 (2)
3 c̄) 3 b° ī°	4/4	—
4 ā ī) 3 b°	1/6 (2)	3/7
4 ā ī°) 4 ā ī	1/7 (1)	2/3
4 ā ī°) 4 b̄	5/6	2/4

TABLE 64. The proportions of the earlier insertion of 10 costellae relative to 10 others (with the number of valves in which both costellae originated at the same growth stage in brackets) for samples of *Reuschella* cf. *horderleyensis* Bancroft (A) and *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 65

	A	B
l̄ mm. (var. l)	11·64 (20·401)	7·05 (10·975)
w̄ mm. (var. w)	16·76 (39·667)	10·52 (22·092)
r	0·989	0·965
a (var. a)	1·394 (0·00304)	1·419 (0·0066)

TABLE 65. Statistics of length (l) and maximum width (w) of 16 brachial valves of *Reuschella* cf. *horderleyensis* Bancroft (A) and 23 brachial valves of *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 66

	A	B
l̄ mm. (var. l)	13·27 (23·93)	11·66 (32·488)
th̄ mm. (var. th)	4·35 (3·931)	3·21 (2·563)
r	0·91	0·936
$\log_e$ l̄ (var. $\log_e$ l)	2·5219 (0·1272)	2·349 (0·2142)
$\log_e$ th̄ (var. $\log_e$ th)	1·3758 (0·1887)	1·0551 (0·2223)
r_e	0·931	0·941
α (var. α)	1·218 (0·00988)	1·019 (0·00516)

TABLE 66. Statistics of length (l) and depth (th) of 22 brachial valves of *Reuschella* cf. *horderleyensis* Bancroft (A) and 25 brachial valves of *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 67

	A		B	
$\bar{l}$ mm. (var. l)	14·68	(19·123)	12·54	(38·679)
$\bar{c}$ mm. (var. c)	2·53	(0.587)	2·60	(1·112)
r	0·932		0·92	
$\log_e \bar{l}$ (var. $\log_e$ l)	2·6437	(0·0856)	2·4189	(0·2199)
$\log_e \bar{c}$ (var. $\log_e$ c)	0·8841	(0·881)	0·8791	(0·1528)
r_e	0·93		0·945	
α (var. α)	1·014	(0·00397)	0·8336	(0·0031)

TABLE 67. Statistics of length of brachial valve (l) and length of cardinalia (c) for 37 specimens of *Reuschella* cf. *horderleyensis* Bancroft (A), and 26 specimens of *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 68

	A		B	
$\bar{l}$ mm. (var. l)	2·6	(0·589)	2·57	(1·13)
$\bar{w}$ mm. (var. w)	4·86	(1·251)	4·14	(3·19)
r	0·809		0·911	
$\log_e \bar{l}$ (var. $\log_e$ l)	0·9358	(0·0837)	0·8649	(0·1579)
$\log_e \bar{w}$ (var. $\log_e$ w)	1·5551	(0·0517)	1·3553	(0·1707)
r_e	0·829		0·904	
α (var. α)	0·7859	(0·00841)	1·039	(0·00823)

TABLE 68. Statistics of length (l) and maximum width (w) of cardinalia of 25 specimens of *Reuschella* cf. *horderleyensis* Bancroft (A) and 26 specimens of *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 69

$\bar{l}$ mm. (var. l)	15·39	(15·362)
$\bar{s}\bar{c}$ mm. (var. sc)	7·48	(3·174)
r	0·942	
a (var. a)	0·4546	(0·0013)

TABLE 69. Statistics of length of brachial valve (l) and length of adductor scar (sc) for 20 specimens of *Reuschella* cf. *horderleyensis* Bancroft.

TABLE 70

	A		B	
$\bar{l}$ mm. (var. l)	13·9	(13·538)	11·48	(33·636)
$\bar{th}$ mm. (var. th)	4·25	(1·058)	4·01	(3·394)
r	0·836		0·916	
a (var. a)	0·2796	(0·00214)	0·3176	(0·00108)

TABLE 70. Statistics of length (l) and thickness (th) of 13 pedicle valves of *Reuschella* cf. *horderleyensis* Bancroft (A) and of 17 pedicle valves of *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 71

	A		B	
$\bar{l}$ mm. (var. l)	14·63	(22·351)	14·5	(31·702)
$\bar{sc}$ mm. (var. sc)	5·38	(4·206)	4·9	(3·932)
r	0·92		0·972	
a (var. a)	0·4338	(0·00111)	0·3521	(0·00038)

TABLE 71. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for 28 specimens of *Reuschella* cf. *horderleyensis* Bancroft (A) and for 21 specimens of *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 72

	A		B	
$\bar{l}$ mm. (var. l)	5·7	(4·445)	4·88	(3·756)
$\bar{w}$ mm. (var. w)	4·67	(1·544)	3·93	(1·804)
r	0·913		0·906	
$\log_e \bar{l}$ (var. $\log_e$ l)	1·6764	(0·1283)	1·5117	(0·1468)
$\log_e \bar{w}$ (var. $\log_e$ w)	1·5068	(0·0687)	1·313	(0·1105)
r_e	0·929		0·917	
α (var. α)	0·7317	(0·00367)	0·8676	(0·00665)

TABLE 72. Statistics of length (l) and maximum width (w) of ventral muscle scars of 22 pedicle valves of *Reuschella* cf. *horderleyensis* Bancroft (A) and of 20 pedicle valves of *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 73

	A		B	
$\bar{l}$ mm. (var. l)	14·23	(20·283)	15·65	(35·826)
$\bar{dl}$ mm. (var. dl)	2·98	(0·887)	3·15	(1·759)
r	0·84		0·914	
$\log_e \bar{l}$ (var. $\log_e$ l)	2·6077	(0·0953)	2·6825	(0·1362)
$\log_e \bar{dl}$ (var. $\log_e$ dl)	1·0442	(0·0953)	1·0658	(0·1631)
r_e	0·868		0·909	
α (var. α)	1·0	(0·00797)	1·095	(0·01096)

TABLE 73. Statistics of length of pedicle valve (l) and length of dental lamellae (dl) for 33 specimens of *Reuschella* cf. *horderleyensis* Bancroft (A) and for 21 specimens of *Reuschella horderleyensis undulata* subsp. nov. (B).

Family HETERORTHIDAE Schuchert & Cooper 1931

Genus ***HETERORTHIS*** Hall & Clarke 1892

TYPE SPECIES. *Orthis clytie* Hall by original designation of Hall & Clarke (1892 : 409).

Heterorthis alternata (J. de C. Sowerby)
(Pl. 9, figs. 1–6, 8, 9)

1839 *Orthis alternata* J. de C. Sowerby : 638, pl. 19, fig. 6.
1871 *Orthis alternata* J. de C. Sowerby ; Davidson : 264, pl. 31, figs. 1–8.

Diagnosis. Subcircular, plano- to concavo-convex *Heterorthis* with gently and evenly convex pedicle valve about one-sixth as deep as long and a brachial valve, commonly plane, about seven-tenths as long as wide, radial ornamentation finely costellate, commonly 3–4 ribs per mm., 10 mm. anterior of umbo, costellae sporadically accentuated ; ventral interarea apsacline with narrow, open delthyrium, dorsal interarea shorter, anacline with angular chilidium covering postero-dorsal surface of cardinal process ; ventral muscle field flabellate, more than two-thirds as long as pedicle valve and slightly broader than long, consisting of pair of semi-oval adjustor scars, disposed posteriorly of diductors, on either side of small pedicle callist, heart-shaped pair of adductor impressions extending forward of umbo for about three-tenths the length of valve, and pair of large diductor scars, including two divergent submedian lobes separated at their tips by a distance over two-fifths the length of valve and pair of smaller, semi-oval, lateral lobes ; ventral pallial sinus pattern probably lemniscate ; cardinal process, high, narrow, rarely encased in massive secondary deposits, ancillary ridges low when present, brachiophores simple, narrowly divergent with bases extending anteriorly for over one-seventh the length of valve ; dorsal adductor field oval, quadripartite deeply impressed especially posteriorly and extending anterior of umbo for over two-fifths the length of valve ; dorsal pallial sinus lemniscate ; subperipheral rims developed in interiors of both adult valves.

Material (Figured).	length	width (mm.)
Internal mould of pedicle valve (BB.28901)	23·0	29·0
External mould of pedicle valve (BB.29134)	21·0	—
External mould of brachial valve (BB.28903)	24·0	32·0
Internal mould of brachial valve (BB.28904)	18·0	24·0
Internal mould of pedicle valve (BB.28905)	22·0	28·0
Internal mould of brachial valve (BB.28906)	22·5	26·0
Incomplete internal mould of pedicle valve (BB.28907)	—	—
Incomplete internal mould of brachial valve (BB.28902)	7·0	—

Horizon and locality. Upper Longvillian Substage : all specimens from the Alternata Limestone exposed at Soudley Quarry, 2 miles south-east of Church Stretton, Shropshire.

Heterorthis cf. *retrorsistria* (M'Coy)

(Pl. 9, figs. 7, 10–17)

1852 *Orthis retrorsistria* M'Coy : 224, pl. 1H, figs. 12, 13.
1871 *Orthis alternata* Sow. var. *retrorsistria* M'Coy ; Davidson : 265, pl. 36, figs. 39–42.

Diagnosis. Subcircular, gently convexo- to concavo-convex *Heterorthis* with an evenly convex pedicle valve less than one-third as deep as long and brachial valve, more commonly flat, less than three-quarters as long as wide and rarely faintly sulcate antero-medianly ; radial ornamentation finely costellate, commonly 4 ribs per mm., 10 mm. anterior of umbo, costellae sporadically thickened ; ventral interarea apsacline with narrow, open delthyrium, dorsal interarea shorter, anacline with subangular chilidium covering postero-dorsal surface of cardinal process ; ventral muscle field variable, flabellate, about two-thirds as long as pedicle valve and about four-fifths as wide as long, including an oval to cordate pair of adductor scars commonly deeply impressed and extending anterior of umbo for about three-tenths the length of valve, submedian diductor lobes wide, separated at their anterior tips by a distance nearly one-half the length of valve, lateral diductor lobes narrow, strip-like, adjustors obscure, pedicle callist well-defined ; ventral pallial sinus probably lemniscate ; cardinal process of adult valves, massive, semi-ovoid commonly ankylosed to high ancillary buttresses, brachiophores simple divergent with bases extending anteriorly for about one-sixth the length of valve ; dorsal adductor scars, oval and quadripartite, deeply impressed especially posteriorly and extending anterior of umbo for nearly one-half the length of valve ; dorsal pallial sinus lemniscate ; subperipheral rims developed in interiors of both adult valves.

Material (Figured).	length	width (mm.)
Internal mould of brachial valve (BB.28908)	15·5	21·5
External mould of brachial valve (BB.28909)	16·5	—
Internal mould of pedicle valve (BB.28910)	7·5	9·5
External mould of brachial valve (BB.28911)	—	—
External mould of pedicle valve (BB.28912)	—	16·5
External mould of brachial valve (BB.28913)	16·0	21·0
Internal mould of pedicle valve (BB.28914)	14·0	18·0
Internal mould of brachial valve (BB.28916)	7·2	—
Internal mould of brachial valve (BB.28954)	3·0	4·8

Horizon and locality. Allt Ddu Group : all specimens from mudstones exposed on the western slopes of Coed Mawr, 1,200 ft. west-north-west of Rhiwlas House.

Discussion. Since the publication of M'Coy's description of *Heterorthis retrorsistria* (M'Coy 1852) there have been some misgivings on the validity of this species. Davidson (1871 : 265), followed Salter, in believing the stock to be a small variety of *H. alternata* and simply reported without comment M'Coy's contention that the " backward curving of the lateral striae to terminate on the hinge-line " was systematically important. As Bancroft (1945 : 239) pointed out this is not a reliable feature exclusive to *H. retrorsistria* and since heterorthids, morphologically indistinguishable from the type specimens of *H. retrorsistria*, occur abundantly in the Lower Allt Ddu, a sample of them has been compared with one of *H. alternata* from the Upper Longvillian of Shropshire.

Data on shell shape and profile are given in Tables 74–81 and they show that the brachial valves of both species were affected by allometry, but that *H. retrorsistria* grew longer, relative to width, faster than *H. alternata* and a comparison of the growth axes, α, showed that the difference is significant ($p < \cdot 01$). The pedicle valves of *H. retrorsistria* are also more strongly convex than those of *H. alternata* due not to any acceleration in growth rate, but to an inherently greater depth of the valve for the indices of inherent shape, b, were significantly different at the 5% level. The differences in the profiles of the brachial valves are more difficult to assess contrary to the assertion of Bancroft (1945 : 239). In both samples the valves may be planar, slightly convex or gently concave although the last condition was usually a late growth modification of a juvenile planar attitude. These three profiles were displayed respectively by 11, 15 and 16 valves of *H. retrorsistria* and by 1, 21 and 3 valves of *H. alternata* so that although those of the former were more variable in convexity, planar valves were commonest in both samples. The same caution must also be exercised over the use of radial ornamentation for specific diagnosis. The pattern is fundamentally the same in both samples but at 10 mm. anterior of the dorsal umbones, counts of 3, 4 and 5 costellae per mm. were obtained in 4, 21 and 15 specimens of *H. retrorsistria* and 7, 8 and 1 of *H. alternata* respectively showing that the ribbing of *H. retrorsistria* tended to be finer but not significantly so.

Internally, differences occur in both valves. The ventral muscle field of *Heterorthis* is highly characteristic and in respect of relative dimensions there are no important differences between the two species either in differential growth or in indices of residual shape (Tables 78–81). Thus the muscle fields of both samples are comparable in their maximum widths relative to their maximum lengths but this statistical similarity conceals a fundamental contrast in the disposition of their constituents. In *H. alternata*, the submedian diductor lobes are narrow, parallel-sided impressions and the maximum width of the entire field is increased by the distension of the lateral lobes as a pair of flanking, semi-oval indentations. In *H. retrorsistria* the lateral lobes are very much reduced and the maximum width is subtended between the lateral edges of the submedian lobes which are splayed out antero-laterally.

TABLE 74

	A	B
$\bar{l}$ mm. (var. l)	8·92 (21·265)	11·89 (36·719)
$\bar{w}$ mm. (var. w)	12·43 (37·155)	16·95 (57·655)
r	0·986	0·986
$\log_e \bar{l}$ (var. $\log_e$ l)	2·0699 (0·2367)	2·3592 (0·2311)
$\log_e \bar{w}$ (var. $\log_e$ w)	2·4126 (0·2151)	2·7387 (0·1831)
r_e	0·996	0·994
α (var. α)	0·9534 (0·00013)	0·8901 (0·00026)

TABLE 74. Statistics of the length (l) and maximum width (w) of 59 brachial valves of *Heterorthis retrorsistria* (M'Coy) (A) and 38 brachial valves of *H. alternata* (J. de C. Sowerby) (B).

TABLE 75

	A	B
$\bar{l}$ mm. (var. l)	13·92 (7·312)	17·46 (32·314)
$\bar{sc}$ mm. (var. sc)	6·4 (1·74)	7·63 (7·813)
r	0·929	0·803
a (var. a)	0·4879 (0·0009)	0·4917 (0·00277)

TABLE 75. Statistics of the length of brachial valves (l) and length of the adductor scars measured from the umbones (sc) for 38 specimens of *Heterorthis retrorsistria* (M'Coy) (A) and 33 of *H. alternata* (J. de C. Sowerby) (B).

TABLE 76

	A	B
$\bar{l}$ mm. (var. l)	13·17 (11·754)	17·52 (33·251)
$\bar{c}$ mm. (var. c)	2·05 (0·404)	2·51 (0·809)
r	0·832	0·825
a (var. a)	0·1854 (0·00028)	0·156 (0·00026)

TABLE 76. Statistics of the length of brachial valves (l) and length of cardinalia (c) for 41 specimens of *Heterorthis retrorsistria* (M'Coy) (A) and 32 of *H. alternata* (J. de C. Sowerby) (B).

TABLE 77

	A	B
$\bar{l}$ mm. (var. l)	12·54 (14·134)	17·58 (27·062)
$\bar{th}$ mm. (var. th)	3·75 (1·53)	3·00 (0·764)
r	0·786	0·76
a (var. a)	0·3289 (0·00172)	0·168 (0·00596)

TABLE 77. Statistics of the length (l) and thickness (th) of 26 pedicle valves of *Heterorthis retrorsistria* (M'Coy) (A) and of 22 pedicle valves of *H. alternata* (J. de C. Sowerby) (B)

TABLE 78

	A		B	
$\bar{l}$ mm. (var. l)	13·98	(8·43)	20·68	(13·859)
$\bar{sc}$ mm. (var. sc)	9·25	(5·681)	14·07	(7·525)
r	0·926		0·958	
a (var. a)	0·8209	(0·00282)	0·7368	(0·00235)

TABLE 78. Statistics of the length of pedicle valves (l) and length of the ventral muscle field measured from the umbo (sc) for 36 specimens of *Heterorthis retrorsistria* (M'Coy) (A) and 36 of *H. alternata* (J. de C. Sowerby) (B).

TABLE 79

	A		B	
$\bar{l}$ mm. (var. l)	10·04	(3·166)	14·37	(7·871)
$\bar{w}$ mm. (var. w)	8·74	(2·688)	14·52	(7·190)
r	0·889		0·956	
a (var. a)	0·9214	(0·01114)	0·9558	(0·00394)

TABLE 79. Statistics of the length (l) and maximum width (w) of the ventral muscle field of 18 specimens of *Heterorthis retrorsistria* (M'Coy) (A) and of 22 of *H. alternata* (J. de C. Sowerby) (B).

TABLE 80

	A		B	
$\bar{l}$ mm. (var. l)	14·97	(3·768)	21·25	(15·089)
$\bar{ad}$ mm. (var. ad)	4·43	(0·483)	6·33	(1·995)
r	0·667		0·819	
a (var. a)	0·3581	(0·00339)	0·3636	(0·00336)

TABLE 80. Statistics of the length of pedicle valves (l) and length of the adductor scars measured from the umbones (ad) of 23 specimens of *Heterorthis retrorsistria* (M'Coy) (A) and of 15 of *H. alternata* (J. de C. Sowerby) (B).

TABLE 81

	A		B	
$\bar{l}$ mm. (var. l)	9·83	(2·86)	14·39	(6·764)
$\bar{di}$ mm. (var. di)	4·61	(0·981)	6·23	(1·259)
r	0·377		0·563	
a (var. a)	0·5857	(0·01398)	0·4314	(0·06359)

TABLE 81. Statistics of the length (l) and anterior separation (di) of the ventral diductor scars of 23 specimens of *Heterorthis retrorsistria* (M'Coy) (A) and of 22 of *H. alternata* (J. de C. Sowerby) (B).

The extensions, anterior of the umbo, of both the brachiophore bases and the deeply impressed adductor scars relative to the length of the brachial valves are again similar in growth and inherent shape (Tables 75, 76). Indeed the dorsal interiors are very much alike in all details except for the form of the cardinal process. In young brachial valves of both species up to about 10 mm. long, the cardinal process is a simple, median plate, subtriangular in outline, with a flattened posterior surface covered dorsally by the chilidium and commonly pointed ventrally. In

H. alternata, the plate stands high above the notothyrial platform and remained so during subsequent growth although the cardinal process itself may have been thickened especially along its ventral surface and in 2 out of 24 specimens outgrowths from the notothyrial platform formed a pair of low flanking buttresses to the cardinal process. In *H. retrorsistria*, these ancillary buttresses were already strongly developed even in valves less than 10 mm. long, where they enveloped the anterior surfaces of the cardinal process. In adult valves they stood only slightly lower than the median plate so that with the excessive thickening that occurred, the entire structure filled the notothyrium as a massive, semi-ovoid, trilobed receptacle for the diductor bases. This pattern seems to have been almost invariable : in only 1 out of 23 adult valves were the ancillary buttresses poorly developed although the median plate was very much thickened and semi-ovoid in ventral outline.

Despite many similarities then, *H. retrorsistria* differs from *H. alternata* in the relatively faster growth in length of the brachial valve, the more highly convex pedicle valve, the small size of the lateral lobes and the splayed ends of the submedian lobes making up the diductor scars and also in the large trilobed cardinal process which fills the notothyrium of adult brachial valves.

Family LINOPORELLIDAE Schuchert & Cooper 1931

Genus ***SALOPIA*** Williams 1955

Type species. *Orthis salteri* Davidson by original designation of Williams (*In* Whittington & Williams 1955 : 409)

Salopia sp

(Pl. 10, figs. 1, 2)

An internal mould of a brachial valve (BB.28915) 6·0 mm. long, 7·5 mm. wide and 2·3 mm. high, has been recovered from calcareous ashes of the Gelli-grîn Group exposed at the south edge of the wood, 850 ft. west of Gelli-grîn Farm. The valve was evidently subcircular in outline, with a short, anacline interarea medianly about one-seventh as long as the valve, and evenly convex in profile with a shallow median sulcus. Judging from the margin of the mould, the surface of the valve was finely multicostellate so that 4 costellae per mm. crenulated the antero-median part of the commissure. The cardinalia consisted of a thin blade-like cardinal process, a pair of strong, divergent brachiophores rectangular in outline and ankylosed to a pair of small fulcral plates that defined semi-ovoid sockets and to a pair of short brachiophore bases which converged on to the median septum at about one-quarter the length of the valve anterior of the umbo. The septum, which stood at mid-point about 0·5 mm. above the valve floor, was narrow and reached almost to the anterior margin. The adductor scars were impressed on either side of the septum, just anterior of the brachiophore bases, as a pair of narrow indentations, extending anteriorly for three-quarters the length of the valve and were divided by narrowly divergent *vascula myaria* into a smaller postero-lateral pair and a larger, subtriangular antero-median pair.

The valve is undoubtedly related to *Salopia salteri* and its subspecies *S. salteri gracilis* (see Whittington & Williams 1955 : 410–411) but it may ultimately prove to belong to a distinct stock with a more strongly convex brachial valve and a better defined median septum.

Superfamily TRIPLESIACEA Quenstedt 1931

Family TRIPLESIIDAE Quenstedt 1931

Genus ***BICUSPINA*** Havlíček 1950

TYPE SPECIES. *Orthis cava* Barrande by original designation of Havlíček (1950 : 87).

Bicuspina spiriferoides (M'Coy)

(Pl. 10, figs. 3–10)

1851 *Strophomena spiriferoides* M'Coy : 402.
1852 *Leptaena* (*Strophomena*) *spiriferoides* (M'Coy) M'Coy : 246.
1871 *Orthis ? spiriferoides* (M'Coy) Davidson : 275, pl. 37, figs. 3–7.

DIAGNOSIS (emended). Subquadrate, unequally biconvex *Bicuspina*, hinge-line wide, cardinal angles rectangular or rarely slightly obtuse ; pedicle valve less than one-half as deep as long, ventral sulcus persistent throughout growth, deep and tending to be flat-bottomed with parallel sides, just over one-third as wide as long ; brachial valve just over two-thirds as long as wide and over one-half as deep as long with high, median, flat-topped, parallel-sided fold ; ventral interarea curved, apsacline, pseudodeltidium folded into narrow arch medianly, dorsal interarea obsolete ; radial ornamentation consisting of fine costellae, rounded in transverse profile, having wavelength of about 0·5 mm. and arising either by branching or intercalation from up to 11 primary costae on either flank and 3 in sulcus ; concentric ornamentation very finely developed, consisting of about 7 lamellae per mm., about 10 mm. anterior of umbo ; pedicle tube slightly curved, just over one-quarter as long as pedicle valve, teeth well developed, pointed, supported by long, slightly divergent dental lamellae extending anteriorly for about one-third the length of valve along its floor and tending to become obscured in adult shells by excessive secondary shell secretion ; ventral muscle field extending forward of ventral umbo for nearly two-thirds the length of pedicle valve and consisting of pair of broad, semi-oval, centrally-placed adductor scars and pair of subtriangular, diductor scars extending well forward of adductors but not enclosing them ; ventral pallial sinus pattern vaguely impressed, possibly lemniscate, *vascula media* subjacent, arising from anterior end of diductor scars ; cardinal process bilobed with long basal shaft curving posteriorly, saddle small, sockets oblique, widely splayed brachiophores subtriangular and blade-like and disposed subparallel with hinge-line, dorsal adductor scars quadripartite impressed mainly on flanks of fold and segregated by faint low median ridge and normal to it, a pair of strong curved ridges representing traces of *vascula myaria*, anterior adductors subtriangular, about equal in size to subrectangular posterior pair and extending forward of dorsal umbo for over two-fifths the length of valve ; pallial sinus pattern obscure.

		length	width (mm.)
Lectotype.	Internal mould of brachial valve (A.42457*a*)	13·0	23·0
	External mould of incomplete crushed shell (dorsal aspect) (A.42457*b*)	—	—
	Incomplete external mould of pedicle valve (A.42457*c*)	—	—
Other Material	Incomplete internal mould of pedicle valve (A42458)	12·5	—
	Incomplete external mould of brachial valve (BB.29032)	—	—
	Incomplete external mould of pedicle valve (BB.29033)	—	—
	Incomplete internal mould of pedicle valve (BB.29034)	18·0	—

Horizon and localities. Gelli-grîn Group : lectotypes A.42457–58 from " Limestone schists of Bala "; BB.29033 from calcareous ash crags 75 ft. south of east end of ruined building in Ffridd Bach, south of Maes-meillion ; BB.29034 from calcareous ashes exposed in field 300 ft. south of Y Garnedd Farm ; BB.29032 from calcareous ash crags cropping out just west of a fence 1,100 ft., almost due west of Gelli-grîn Farm.

Discussion. One of the most distinctive brachiopods found in the Caradocian rocks of south Britain is the wide-hinged, spiriferoid-like triplesiaceid first recorded by M'Coy (1851 : 402) as *Strophomena spiriferoides* and now known to belong to a well-distributed generic stock, *Bicuspina* Havlíček. Although European species range from Llandeilian to late Caradocian in age (Havlíček 1950 : 88), it appears that the British species is much more restricted and it is generally supposed to be pre-eminently characteristic of the Longvillian stage although this belief still requires confirmation and in any case it is important to know what precisely is meant by " *Strophomena* " *spiriferoides*.

M'Coy's description is quite exhaustive and although no one can doubt that during its preparation he had the *Bicuspina* kind of shell in mind, it is not accompanied by any illustrations and is clearly a generalized statement covering a number of specimens (twenty-seven of them are still preserved in the Sedgwick Museum) that had been taken from at least eleven localities in North Wales and the Welsh borderlands. In attempting to restrict the species to specimens collected from certain rocks exposed in one locality, no precedence need be attached to his list of occurrences (M'Coy 1851 : 402) which was obviously drawn up without any intention of order. The Bala district, however, was evidently his chief source of material because he records the stock from four distinct exposures, in the vicinity of that town, of what are now known to be ashes and limestones of the Gelli-grîn Group. Moreover, when he issued an almost identical description of the species

(M'Coy 1852 : 246), the only noteworthy additions were two rather stylized drawings of the internal moulds of a brachial (left-hand figure) and a pedicle (right-hand figure) valve. While it is impossible to be certain in this matter, it seems very likely that the right-hand figure was based on a mould (A.42458) recorded as from the " Limestone schists of Bala "; the left-hand figure is probably a composite reconstruction for there is no reasonable model for it among the specimens used by M'Coy. On the strength, then, of this identification and the preponderance of specimens from the Bala district in the collection examined by M'Coy, it is reasonable to choose lectotypes known from lithology and record to have been recovered from the Gelli-grîn Group. The exact locality is conjectural. In both descriptions M'Coy refers to specimens from " schists of Bryn Melyn " as well as those of " Gelli-Grîn ", " Tan y Bwlch y Groes " and " Garnedd Uchaf ". Specimens from the last three outcrops are so identified in the collection, but none is attributed to the Bryn Melyn outcrop and since the lectotypes were chosen from the only lot labelled simply as " Limestone Schists Bala " it could well be that these actually were taken from the ashy limestones cropping out near Bryn Melyn.

There is not a great deal more to be said about the morphological variability of the species as thus restricted because, although moulds of both valves are common enough in the Gelli-grîn Group, they are mostly too deformed to be used for more than generic identification and the proportions given in the diagnosis represent averages for between 2 and 5 specimens. The radial ornamentation, however, does require some comment. It consists of evenly rounded costellae with a wavelength of 0·3, 0·4 and 0·5 mm., 10 mm. antero-medianly of the ventral umbones of 2, 2 and 4 specimens respectively. These consistent measurements are a reflection of the regularity with which new costellae arise either by intercalation or by branching from the 20 or so primary costae originating at the umbo. The complex pattern of ribs within the sulcus (a complementary arrangement is to be expected on the fold) has been traced from its origin in only two valves. In both, a median costa arising at the beak bifurcated to form a submedian pair and within 2 mm. another median rib had appeared, either by intercalation or by branching from the left submedian one, so that basically a triad of costae with ancillary branches and intercalations occupied the floor of the sulcus. In addition to these, internal branches from the primary costae occupying the shoulders of the sulcus " migrated ", with the enlargement of the valve, down the sides ultimately to occupy the lateral segments of the floor. The first pair of these lateral branches can arise early but they are invariably later than the dichotomy of the original median primary and in 10 out of 12 valves they also appeared later than the second median costa.

Moulds of *Bicuspina* are also found in the highest Allt Ddu sandstones and mudstones and very rarely in siltstones just above the Frondderw Ash ; at present they are indistinguishable from *B. spiriferoides* s.s. The Czechoslovakian species *B. cava* (Barrande) and *B. multicostellata* Havlíček, which have been identified in Llandeilo and Lower Caradoc rocks (see Havlíček 1950 : 88–89) differ greatly from the British species in the very much greater relative length of the valves, the weakness or even absence of the fold and sulcus and the fineness of the radial ornamentation.

Genus ***OXOPLECIA*** Wilson 1913

TYPE SPECIES. *Oxoplecia calhouni* Wilson by original designation of Wilson (1913 : 81).

Oxoplecia sp.

(Pl. 10, figs. 11–13, 17)

DESCRIPTION. Subcircular, biconvex *Oxoplecia* with a short hinge-line and obtuse cardinal angles, brachial valve over four-fifths as long as wide and over one-quarter as deep as long with a high rounded fold less than one-half as wide as the valve is long, sulcus in pedicle valve correspondingly deep with steep lateral slopes ; concentric lamellae on the shell-exterior, consistently developed and fine, numbering about 9 per mm., 5 mm. anterior of the ventral umbo ; radial ornamentation well developed within 2 mm. of the umbones and consisting of well-rounded costae attaining a wavelength of up to 0·7 mm. before dividing, in the sulcus up to 5 ribs appear in valves up to 8 mm. long but at least 2 of these can arise by branching or implantation ; on the fold 3 costae first developed but the median and right lateral ones branched dichotomously within a few millimetres of the dorsal umbo so that with further branching as many as 9 costae and costellae occur on the crest of the fold ; as many as 9 costae occur on each flank with the pair adjacent to the fold or sulcus giving rise to freely developed external and internal costellae ; dental lamellae short and divergent ; cardinal process bifurcating early, socket ridges ankylosed to the base of the cardinal process and subtriangular in outline, dorsal adductor muscle field quadripartite about the fold with the larger subtriangular anterior pair separated from the posterior by a pair of curved depressions.

MATERIAL (Figured).	length	width (mm.)
Incomplete external mould of pedicle valve (BB.29035)	9·0	—
Incomplete internal mould of pedicle valve (BB.24622)	—	—
Incomplete external mould of brachial valve (BB.29037)	12·0	—
Incomplete internal mould of brachial valve (BB.29038)	—	—

HORIZON AND LOCALITIES. Gelli-grîn Group : all specimens from calcareous ash crags 75 ft. south of east end of ruined building in Ffridd Bach, south of Maes-meillion.

DISCUSSION. A few incomplete moulds of a species of *Oxoplecia* have been recovered from the Gelli-grîn Group and have been described because they differ importantly from the other species recorded from the Caradocian rocks of North Wales, namely *O. mutabilis* Williams (see Whittington & Williams 1955 : 411) from the Derfel limestone, especially in the relatively wider dorsal fold and in the development of radial ornamentation in early stages of growth. In respect of these features, the Bala moulds are like *Oxoplecia dorsata* (Hisinger) as redescribed by Öpik (1930 : 200) but are less quadrate in outline and until the significance of this difference can be assessed it seems appropriate not to assign a specific status to them.

Superfamily CLITAMBONITACEA Winchell & Schuchert 1893

Family CLITAMBONITIDAE Winchell & Schuchert 1893

Genus ***VELLAMO*** Öpik 1930

TYPE SPECIES. *Orthis verneuili* Eichwald by original designation of Öpik (1930 212).

Vellamo sp.

(Pl. 10, figs. 14, 18)

The external and internal moulds (BB.28965, BB.29133) of a broken pedicle valve, collected from mudstones of the Allt Ddu Group on the moorland 1,950 ft. east of Llaithgwm Farm, are the only clitambonitaceid remains yet recorded in the Caradocian rocks of the Bala district. The valve which was about 9 mm. long and 5·5 mm. deep, was transversely subpentagonal in outline but asymmetrical due to impeded growth of the left half, and subpyramidal in profile with a slight median sulcus indenting the anterior commissure. The surface was ornamented by strong costae and costellae, rounded in profile and with a wave-length of about 0·5 mm. at the anterior margin. About 20 arose within 3 mm. of the umbo and thereafter branched evenly to be interrupted at irregular intervals by " growth lines ". Judging from better preserved parts of the external mould, the shell surface was also ornamented by fine concentric lines with an incidence of 8 between 3 and 4 mm. anterior of the umbo, but these are never extravagantly developed as lamellae in the manner of *Clitambonites* and the valve is certainly best assigned to the genus *Vellamo*. The internal mould is incomplete and shows only the slot for a median ridge which must have extended anterior of the spondylium in the manner typical of the clitambonitids.

In both profile and outline as well as the median sulcus and the multicostellate radial ornamentation, the valve is clearly related to the *V. pyramidalis* (Pahlen) species group (see Öpik 1930 : 213–217) but more material will have to be obtained before specific identification is attempted.

Superfamily PLECTAMBONITACEA Kozlowski 1929

Family LEPTELLINIDAE Ulrich & Cooper 1936

Genus ***LEPTESTIINA*** Havlíček 1952

TYPE SPECIES. *Leptestiina prantli* Havlíček by original designation of Havlíček (1952 : 13).

Leptestiina oepiki (Whittington)

(Pl. 10, figs. 15, 16, 19–21)

1938 *Sampo oepiki* Whittington : 255, pl. 10, figs. 15–16, pl. 11, fig. 10.

DIAGNOSIS (emended). Semi-circular and evenly concavo-convex *Leptestiina* with pedicle valve almost three-fifths as long as wide and over two-fifths as deep as long ; radial ornamentation unequally parvicostellate with fine costellae, about

7 or 8 per mm., segregated into sectors up to 1·5 mm. wide by conspicuous, thickened ribs three of which, a lateral pair subtending an angle of about 90° and symmetrical about a median one, arise at the umbo, additional thickened costellae arise beyond the 1 mm. growth stage maintaining the regularity of the sectors so that in valves 5 mm. long, about nine of varying length occur ; concentrically arranged, interrupted comae incipiently developed especially on ventral surface ; ventral interarea apsacline, pseudodeltidium small and apical, foramen closed ; dorsal interarea hypercline, chilidial plates well developed ; teeth and accessory nodes buttressed by short receding dental lamellae, ventral muscle field transversely subpentagonal in outline, extending anteriorly for less than one-third the length of pedicle valve and about three-quarters as long as wide, adductor field lanceolate, commonly divided medianly by low ridge and deeply inserted, especially posteriorly, into thick shell substance of umbonal cavity, diductor scars almost meeting anteriorly to enclose adductor scar and divided into pair of narrow, submedian lobes encroaching on *vascula media* and broad pair of lateral lobes, ventral pallial sinus pattern lemniscate ; cardinal process consisting of simple, median ridge supported by thickened notothyrial platform passing anteriorly into low, broad median ridge which bifurcates about the deep incision of the lophophore platform, socket ridges widely disposed, subparallel with hinge-line to define a pair of oval sockets ; lophophore platform about three-fifths as long as brachial valve, and about three-quarters as long as wide, defined posteriorly as pair of widely divergent ridges confluent with bases of socket ridges but strongly undercut and medianly incised anteriorly and ornamented by about 20 radiating ridges ; adductor scars vaguely impressed on either side of median ridge ; dorsal pallial sinus pattern lemniscate.

Material (Figured).	length	width (mm.)
Deformed internal mould of pedicle valve (BB.28886)	7·0	9·5
Internal mould of pedicle valve (BB.28890)	6·0	9·0
External mould of brachial valve (BB.28889)	5·0	10·0
External mould of pedicle valve (BB.28888)	5·5	—
Internal mould of brachial valve (BB.28891)	5·5	—

Horizon and localities. Gelli-grîn Group : BB.28886 from calcareous ashes exposed on the north side of the central outlier of Rhiwlas Limestone on Creigiau Bychain ; BB.28888–91 from calcareous ashes above the limestone in the old quarries in Ffridd Bach, south of Maes-meillion.

Discussion. This species occurs rarely in the Longvillian of Wales and the Welsh Borderlands and has been redescribed because the moulds obtained from the Gelli-grîn Group were adequate in both preservation and numbers to show that

the stock is more appropriately assigned to *Leptestiina* and to provide some comparative evaluation of its general morphology. The pedicle valves were almost semi-circular in outline and strongly and evenly convex with a mean percentage length relative to width (with variance) of 57·8 (66·43) for 8 moulds and a mean percentage depth relative to length of 44 (range 38–52) for 3 moulds. The ornamentation is usually poorly preserved but the sporadic occurrence of comae with the suggestions of a concentric disposition and especially the segregation of the fine costellae into sectors by the excessive thickening of regularly spaced costae and costellae are noteworthy. The ventral muscle field is unexceptional in arrangement : in 5 internal moulds the mean percentage length relative to that of the valve was 31·0 (variance 24·0) and its transversely subpentagonal outline is reflected in a mean percentage length relative to width of 75·4 (variance 154·67) in 9 moulds. The interior of the brachial valve was dominated by the deeply incised subrectangular lophophore platform with semi-circular undercut anterior margins. In 3 dorsal internal moulds the mean percentage length of the lophophore platform relative to that of the valve was 60·7 (range 56–64) and in 9 moulds the mean percentage length of the platform relative to width (with variance) was 76·2 (59·75).

The species is closely related to *Leptestiina derfelensis* (Jones 1928 : 479–481 ; see also Whittington & Williams 1955 : 415) and in the absence of good samples it is difficult to assess the importance of those differences which appear to distinguish the two stocks. Certainly in shell outline, both are comparable and although *L. oepiki* is possibly more deeply convex and bears umbonally 3 thickened costae in contrast to 5 reported for *L. derfelensis*, better preserved material may show that the differences are not really significant. Internally, the ventral muscle field may prove to be longer relative to the length of the valve but the most important distinction is probably in the different shapes of the lophophore platform which is less than three-fifths as long as wide in *L. derfelensis*.

Family SOWERBYELLIDAE Öpik 1930

Genus ***SOWERBYELLA*** Jones 1928

Type species. *Leptaena sericea* J. de C. Sowerby by original designation of Jones (1928 : 384).

Sowerbyella sericea (J. de C. Sowerby)

(Pl. 11, figs. 1–9 ; Text-figs. 11, 12)

1839 *Leptaena sericea* J. de C. Sowerby: 636, pl. 19, fig. 1.
1928 *Sowerbyella sericea* (J. de C. Sowerby) Jones : 414, pl. 21, figs. 1–4.

Diagnosis (emended). Semi-circular *Sowerbyella* with evenly concavo-convex longitudinal profile rarely modified by low narrow median fold in pedicle valve, cardinal angles acute in young stages of growth but commonly becoming rectangular or even obtuse in adult shells, pedicle valve less than two-thirds as long as wide and

over one-quarter as deep as long ; radial ornamentation unequally parvicostellate commonly with 7 or 8 costellae per mm., 10 mm. antero-medianly of dorsal umbo, segregated into sectors about 0·8 mm. wide, postero-lateral areas also commonly ornamented by rugae with wavelength of 0·3 mm. disposed acutely to hinge-line and commonly forming 4 pairs extending antero-medianly through sectors of up to 25°, pseudodeltidium and chilidium small, apical ; teeth small, dental lamellae obsolescent in adult shells ; ventral muscle field deeply cordate in outline over three-quarters as long as wide and extending anteriorly for just over one-half the length of pedicle valve, adductor scars small, lanceolate, inserted posteriorly into callist beneath pseudodeltidium, and divided by median septum extending anteriorly for about one-quarter the length of valve, diductor scars widely separated anteriorly and split by divergent *vascula media* ; ventral pallial sinus pattern lemniscate ; cardinalia about one-third as long as wide, extending anteriorly for about one-eighth the length of brachial valve and consisting of median cardinal process fused with chilidial plates and widely divergent socket ridges, notothyrial platform not conspicuously hollowed, submedian septa narrowly divergent, extending anteriorly for nearly three-quarters the length of valve, " lophophore " platform elevated, divided by *vascula myaria* and nearly one-fifth as wide again as length of submedian septa that form its inner boundaries ; low median ridge commonly developed between submedian septa in brachial valves over 5 mm. long ; pallial sinus pattern lemniscate.

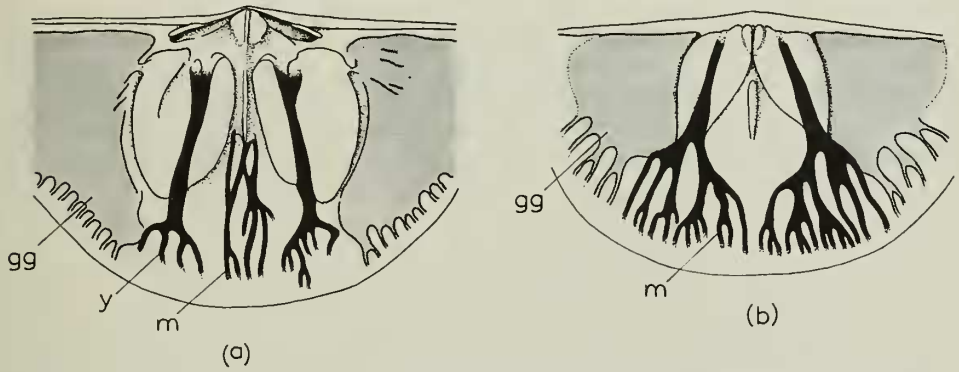

FIG. 11. The dorsal (a) and ventral (b) internal moulds of *Sowerbyella sericea* (J. de C. Sowerby), ×3 approx., showing the pallial sinus patterns : *gg, vascula genitalia* ; *m, vascula media* ; *y, vascula myaria.*

MATERIAL (Figured).	length	width (mm.)
Internal mould of pedicle valve (BB.29064)	8·5	14·0
Internal mould of pedicle valve (BB.29065)	11·0	19·5
Internal mould of pedicle valve (BB.29066)	5·0	9·5

Material (Figured) (*continued*).	length	width (mm.)
Internal mould of brachial valve (BB.29067)	8·0	14·5
Internal mould of brachial valve (BB.29068)	3·6	6·2
Internal mould of brachial valve (BB.29069)	—	21·0
External mould of brachial valve (BB.29070)	3·5	6·0
External mould of brachial valve (BB.29071)	8·0	14·0
External mould of pedicle valve (BB.29072)	10·0	17·0

Horizon and locality. Upper Longvillian Substage : all specimens from the Alternata Limestone exposed at Soudley Quarry, 2 miles south-east of Church Stretton, Shropshire.

Sowerbyella soudleyensis Jones
(Pl. 12, figs. 1–8)

1928 *Sowerbyella sericea* (J. de C. Sowerby) var. *soudleyensis* Jones : 417, pl. 21, figs. 5, 6.

Diagnosis. Semi-circular *Sowerbyella* with concavo-convex profile commonly modified by narrow median fold in pedicle valve, cardinal angles acute to rectangular in adult shells, pedicle valve just over one-half as long as wide and about one-third as deep as long ; radial ornamentation unequally parvicostellate commonly with 8 costellae per mm., 10 mm. antero-medianly of dorsal umbo, segregated in sectors about 1 mm. wide, postero-lateral areas also commonly ornamented by rugae with wavelength of 0·3 mm., disposed acutely to hinge-line and commonly forming 3 pairs extending antero-medianly through sectors of up to 25°, pseudodeltidium and chilidium small, apical ; teeth small, dental lamellae obsolescent in adult shells, ventral muscle field deeply cordate in outline about three-quarters as long as wide and extending anteriorly for just over one-half the length of pedicle valve, adductor scars small, lanceolate, inserted posteriorly into callist beneath pseudodeltidium and divided by median septum extending anteriorly for about one-quarter the length of valve, diductor scars widely separated anteriorly and split by divergent *vascula media* contributing to a lemniscate pallial sinus pattern ; cardinalia about one-third as long as wide, extending anteriorly for about one-eighth the length of brachial valve and consisting of median cardinal process fused with chilidial plates and widely divergent socket ridges, notothyrial platform commonly not conspicuously hollowed ; submedian septa narrowly divergent, extending anteriorly for about seven-tenths the length of valve, " lophophore " platform elevated and

tending to be undercut along its anterior margin and nearly one-third as wide again as the length of submedian septa that form its inner boundary ; low median ridge commonly developed between submedian septa in brachial valves over 5 mm. long ; pallial sinus pattern lemniscate.

Material (Figured).	length	width (mm.)
Internal mould of pedicle valve (BB.29073)	8·0	12·5
Exfoliated exterior of pedicle valve (BB.29074)	7·2	—
Internal mould of pedicle valve (BB.29075)	5·5	11·5
External and internal moulds of pedicle valve (BB.29076–77)	3·2	6·0
External and internal moulds of brachial valve (BB.29078–79)	2·8	—
Internal mould of brachial valve (BB.29080)	5·0	9·5
External mould of brachial valve (BB.29081)	7·0	14·0
External mould of brachial valve (BB.29082)	5·8	10·0

Horizon and locality. Lower Longvillian Substage : all specimens topotypic with those used by Jones (1928 : 417–418) to establish the variety *S. sericea* var. *soudleyensis* and obtained from green-weathering sandstones exposed in an old quarry on the roadside south of Whittingslow, Shropshire.

Sowerbyella musculosa sp. nov.
(Pl. 11, figs. 18–27)

Diagnosis. Semi-circular *Sowerbyella* with pedicle valve just over one-half as long as wide and nearly two-fifths as deep as long with evenly concavo-convex longitudinal profile, rarely subcarinate or obscurely uniplicate, cardinal angles rarely rectangular or obtuse in adult shells ; radial ornamentation unequally parvicostellate commonly with 9 costellae per mm., 10 mm. antero-medianly of dorsal umbo, and commonly segregated into sectors about 0·7 mm. wide ; postero-lateral areas also commonly ornamented by 3 pairs of short rugae with wavelength of about 0·3 mm. and disposed acutely to hinge-line ; ventral muscle field deeply cordate in outline, nearly as long as wide and extending anteriorly for less than one-half the length of pedicle valve, median septum separating small lanceolate adductor scars, extending anteriorly for about one-quarter the length of valve and merging posteriorly with callist ; cardinalia over two-fifths as long as wide and extending anteriorly for less than one-fifth the length of brachial valve, notothyrial

platform tending to be hollowed, submedian septa narrowly divergent, extending anteriorly for about two-thirds the length of valve commonly containing median ridge in valves over 2·5 mm. long, " lophophore " platform strongly elevated, over one-third as wide again as the length of submedian septa.

		length	width (mm.)
Holotype.	External and internal moulds of pedicle valve (BB.29083–84)	4·2	7·5
Paratypes.	External and internal moulds of pedicle valve (BB.29085–86)	3·0	5·3
	External and internal moulds of brachial valve (BB.29087–88)	2·8	6·0
	Internal mould of brachial valve (BB.29089)	5·5	10·0
	External mould of pedicle valve (BB.29090)	3·2	7·0
	Incomplete internal mould of pedicle valve (BB.28895)	6·5	—
	External mould of pedicle valve (BB.29091)	4·5	8·0
	External mould of pedicle valve (BB.29092)	5·5	—

Horizon and locality. Allt Ddu Group : all specimens from fine sandstones and mudstones immediately below the Pont-y-Ceunant Ash and exposed in crags north of the drive to Y Garnedd Farm.

Sowerbyella sericea (J. de C. Sowerby) *permixta* subsp. nov.
(Pl. 11, figs. 10–17)

Diagnosis. Semi-circular *Sowerbyella* with pedicle valve over one-half as long as wide and about one-third as deep as long with evenly concavo-convex longitudinal profile, rarely subcarinate or shallowly uniplicate ; cardinal angles rarely rectangular or obtuse in adult shells ; radial ornamentation unequally parvicostellate commonly with 9 costellae per mm., 10 mm. antero-medianly of dorsal umbo, and segregated into sectors about 0·6 mm. wide ; postero-lateral areas also commonly ornamented by 4 pairs of short rugae, with wavelength of about 0·3 mm. and disposed acutely to hinge-line ; ventral muscle field deeply cordate in outline nearly four-fifths as long as wide and extending anteriorly for about one-half the length of pedicle valve, median septum separating small, lanceolate adductor scars, extending anteriorly for nearly one-quarter the length of valve and merging posteriorly with callist ; cardinalia nearly two-fifths as long as wide and extending anteriorly for about

one-eighth the length of brachial valve, notothyrial platform not greatly hollowed, submedian septa narrowly divergent, extending anteriorly for about two-thirds the length of valve commonly containing a median ridge in valves over 2·5 mm. long, " lophophore " platform elevated, less than one-fifth as wide again as the length of submedian septa.

		length	width (mm.)
Holotype.	Internal mould of brachial valve (BB.29093)	6·5	12·0
Paratypes.	Internal mould of brachial valve (BB.29094)	3·0	—
	Internal mould of brachial valve (BB.29095)	1·8	3·7
	Internal mould of brachial valve (BB.29096)	4·0	8·0
	External mould of brachial valve (BB.29097)	5·0	10·5
	External mould of brachial valve (BB.29098)	5·0	9·0
	Internal mould of pedicle valve (BB.29099)	6·5	—
	Internal mould of pedicle valve (BB.29100)	8·0	13·5

Horizon and localities. BB.29093–99 from mudstones of the Nant Hir Group exposed in left bank of Nant Hir, 600 ft. north-east of Cefn-y-maes Farm ; BB.29100 from fine sandstones of the Glyn Gower Group exposed as crags in field, 1,100 ft. west of Y Fedw Farm.

Discussion. The genus *Sowerbyella* is well represented at most fossiliferous horizons within the Caradocian successions of the Bala district and three samples, comprising associates of *Dinorthis berwynensis angusta* subsp. nov. and *Heterorthis retrorsistria* (M'Coy) from the upper and lower parts respectively of the Allt Ddu Group as well as a composite lot from the Upper Glyn Gower and Nant Hir Groups have been used to assess any changes that might have taken place. The youngest forms were probably contemporaries of *S. soudleyensis* (Jones) that abounds in the Lower Longvillian rocks of the Welsh Borders. This latter species was originally described by Jones (1928 : 417) as a variety of *S. sericea* (J. de C. Sowerby) but a study of two good collections of topotypic material shows that these two stocks are unlike in a number of features and are better treated as two distinct species in the manner described above. Further, when these are compared with the Bala specimens, it becomes evident that the bulk of the Welsh shells are only slightly different from *S. sericea* whereas those from the top of the Allt Ddu Group are quite distinct from all known stocks and so a new subspecies, *S. sericea permixta*, and a new species, *S. musculosa*, have been proposed in recognition of these differences.

TABLE 82

	A	B	C	D	E
$\bar{l}$ mm	6·85	5·39	3·15	7·1	4·69
(var. l)	(4·66)	(1·997)	(1·093)	(3·504)	(5·668)
$\bar{w}$ mm.	12·2	10·07	6·29	12·55	8·78
(var. w)	(14·458)	(5·253)	(3·49)	(9·658)	(16·478)
r	0·973	0·927	0·969	9·971	0·984
$\log_e \bar{l}$	1·8768	1·651	1·0952	1·9262	1·4306
(var. $\log_e$ l)	(0·0948)	(0·0669)	(0·1044)	(0·0677)	(0·2295)
$\log_e \bar{w}$	2·4549	2·2841	1·7967	2·4996	2·0760
(var. $\log_e$ w)	(0·0929)	(0·0507)	(0·0846)	(0·0602)	(0·1930)
r_e	0·979	0·936	0·978	0·959	0·964
α	0·9899	0·8706	0·9002	0·943	0·9171
(var. α)	(0·00099)	(0·00276)	(0·00121)	(0·00476)	(0·0033)

TABLE 82. Statistics of length (l) and maximum width (w) of 43 pedicle valves of *Sowerbyella sericea* (J. de C. Sowerby) (A), 36 of *S. soudleyensis* Jones (B), 31 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 17 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 20 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).

TABLE 83

	A	B	C	D	E
$\bar{l}$ mm.	7·06	5·15	3·6	6·63	4·94
(var. l)	(3·752)	(1·48)	(1·808)	(5·836)	(5·515)
$\overline{th}$ mm.	2·01	1·79	1·39	2·45	1·58
(var. th)	(0·662)	(0·333)	(0·415)	(1·178)	(0·836)
r	0·819	0·895	0·884	0·957	0·971
$\log_e \bar{l}$	1·9181	1·6117	1·2154	1·8296	1·4955
(var. $\log_e$ l)	(0·0725)	(0·0545)	(0·1310)	(0·1239)	(0·2037)
$\log_e \overline{th}$	0·6239	0·5328	0·232	0·8065	0·3129
(var. $\log_e$ th)	(0·1484)	(0·0988)	(0·1946)	(0·1792)	(0·2889)
r_e	0·807	0·898	0·91	0·95	0·985
α	1·43	1·346	1·219	1·202	1·19
(var. α)	(0·01587)	(0·01098)	(0·008)	(0·01282)	(0·00302)

TABLE 83. Statistics of length (l) and maximum depth (th) of 47 pedicle valves of *Sowerbyella sericea* (J. de C. Sowerby) (A), 34 of *S. soudleyensis* Jones (B), 34 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 13 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 16 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).

TABLE 84

	A	B	C	D	E
$\bar{l}$ mm.	7·03	5·36	3·2	7·29	5·95
(var. l)	(3·875)	(1·756)	(1·699)	(3·929)	(2·563)
$\bar{s}$ mm.	1·72	1·41	0·82	1·66	1·33
(var. s)	(0·219)	(0·15)	(0·158)	(0·218)	(0·131)
r	0·946	0·848	0·84	0·91	0·863
a	0·2377	0·2922	0·305	0·2356	0·2261
(var. a)	(0·00011)	(0·00051)	(0·00082)	(0·00033)	(0·00041)

TABLE 84. Statistics of length of pedicle valve (l) and length of septum within the ventral muscle field (s) for 59 specimens of *Sowerbyella sericea* (J. de C. Sowerby) (A), 50 of *S. soudleyensis* Jones (B), 35 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 31 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 34 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).

TABLE 85

	A	B	C	D	E
$\bar{l}$ mm.	7·06	5·48	3·61	7·4	6·41
(var. l)	(3·964)	(1·916)	(2·397)	(3·524)	(1·676)
$\bar{s}\bar{c}$ mm.	3·68	2·98	1·69	3·84	3·21
(var. sc)	(1·581)	(0·825)	(0·716)	(1·313)	(0·587)
r	0·947	0·963	0·781	0·959	0·919
$\log_e \bar{l}$	1·9159	1·67	1·1992	1·9699	1·8378
(var. $\log_e$ l)	(0·077)	(0·0621)	(0·169)	(0·0631)	(0·0402)
$\log_e \bar{s}\bar{c}$	1·2476	1·0473	0·4131	1·3027	1·1385
(var. $\log_e$ sc)	(0·1105)	(0·0891)	(0·2231)	(0·0856)	(0·0555)
r_e	0·934	0·961	0·8	0·947	0·91
α	1·198	1·198	1·149	1·165	1·175
(var. α)	(0·003)	(0·00239)	(0·02374)	(0·00467)	(0·00719)

TABLE 85. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for 63 specimens of *Sowerbyella sericea* (J. de C. Sowerby) (A), 48 of *S. soudleyensis* Jones (B), 22 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 32 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 35 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).

TABLE 86

	A	B	C	D	E
$\bar{l}$ mm.	3·77	3·12	1·79	3·78	3·17
(var. l)	(1·618)	(0·684)	(0·757)	(0·803)	(0·845)
$\bar{w}$ mm.	4·78	4·08	1·83	4·63	4·06
(var. w)	(2·663)	(1·093)	(0·522)	(1·123)	(1·38)
r	0·961	0·905	0·936	0·976	0·949
$\log_e \bar{l}$	1·2731	1·1039	0·4763	1·3024	1·1133
(var. $\log_e$ l)	(0·1079)	(0·0677)	(0·2118)	(0·054)	(0·0808)
$\log_e \bar{w}$	1·5096	1·3741	0·5318	1·5072	1·3608
(var. $\log_e$ w)	(0·1096)	(0·064)	(0·145)	(0·0507)	(0·0808)
r_e	0·969	0·93	0·945	0·988	0·953
α	1·008	0·9723	0·8274	0·969	1·0
(var. α)	(0·00113)	(0·00376)	(0·00431)	(0·00173)	(0·00655)

TABLE 86. Statistics of length (l) and maximum width (w) of the ventral muscle scar in 57 pedicle valves of *Sowerbyella sericea* (J. de C. Sowerby) (A), 36 of *S. soudleyensis* Jones (B), 19 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 15 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 16 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).

TABLE 87

	A	B	C	D	E
$\bar{l}$ mm.	6·19	5·42	3·05	5·94	5·29
(var. l)	(4·562)	(3·196)	(1·571)	(4·503)	(4·322)
$\bar{s}$ mm.	4·51	3·89	2·10	4·07	3·48
(var. s)	(2·77)	(1·94)	(0·699)	(2·202)	(2·169)
r	0·96	0·974	0·967	0·974	0·968
$\log_e \bar{l}$	1·7668	1·6385	1·037	1·722	1·5941
(var. $\log_e$ l)	(0·1122)	(0·1031)	(0·1562)	(0·1194)	(0·1433)
$\log_e \bar{s}$	1·4426	1·2982	0·6685	1·3412	1·1646
(var. $\log_e$ s)	(0·1274)	(0·1203)	(0·1468)	(0·1248)	(0·1648)
r_e	0·959	0·981	0·975	0·971	0·96
α	1·065	1·08	0·9694	1·022	1·072
(var. α)	(0·00175)	(0·00112)	(0·00101)	(0·0026)	(0·00117)

TABLE 87. Statistics of the length of the brachial valve (l) and the length of the submedian septas from the dorsal umbo of 59 specimens of *Sowerbyella sericea* (J. de C. Sowerby) (A), 41 of *S. soudleyensis* Jones (B), 48 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 25 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 79 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).

TABLE 88

	A	B	C	D	E
$\bar{l}$ mm.	5·12	4·19	2·73	4·18	4·45
(var. l)	(1·713)	(1·317)	(0·526)	(1·126)	(1·36)
$\bar{w}$ mm.	6·05	5·56	3·71	5·34	5·87
(var. w)	(2·485)	(2·698)	(1·376)	(2·055)	(2·862)
r	0·938	0·934	0·914	0·927	0·942
$\log_e \bar{l}$	1·6012	1·3964	0·9699	1·3987	1·4594
(var. $\log_e$ l)	(0·064)	(0·0725)	(0·0687)	(0·0631)	(0·0669)
$\log_e \bar{w}$	1·7671	1·6737	1·2633	1·6404	1·7299
(var. $\log_e$ w)	(0·0659)	(0·0837)	(0·0953)	(0·0696)	(0·0799)
r_e	0·956	0·931	0·943	0·923	0·94
α	1·015	1·074	1·178	1·05	1·093
(var. α)	(0·00286)	(0·0053)	(0·00698)	(0·02334)	(0·00496)

TABLE 88. Statistics of the length of the submedian septa from the dorsal umbo (l) and the width of the " lophophore platform " (w) of 33 specimens of *Sowerbyella sericea* (J. de C. Sowerby) (A), 31 of *S. soudleyensis* Jones (B), 24 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 9 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D), 30 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 30 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).

TABLE 89

	A	B	C	D	E
$\bar{l}$ mm.	6·33	5·07	3·14	6·29	5·21
(var. l)	(3·379)	(2·698)	(1·581)	(2·928)	(3·043)
$\bar{c}$ mm.	0·82	0·62	0·54	0·81	0·68
(var. c)	(0·074)	(0·053)	(0·052)	(0·088)	(0·07)
r	0·797	0·977	0·671	0·917	0·941
$\log_e \bar{l}$	1·8049	1·5734	1·07	1·8032	1·5975
(var. $\log_e$ l)	(0·0808)	(0·0997)	(0·1484)	(0·0715)	(0·1061)
$\log_e \bar{c}$	−0·2507	−0·5426	−0·6982	−0·2736	−0·4561
(var. $\log_e$ c)	(0·1044)	(0·1292)	(0·164)	(0·1257)	(0·1407)
r_e	0·81	0·966	0·686	0·929	0·935
α	1·137	1·139	1·051	1·326	1·152
(var. α)	(0·01169)	(0·00321)	(0·01541)	(0·02007)	(0·00371)

TABLE 89. Statistics of the length of the brachial valve (l) and the anterior extension of the socket ridges or brachiophores from the dorsal umbo (c) in 40 specimens of *Sowerbyella sericea* (J. de C. Sowerby) (A), 29 of *S. soudleyensis* Jones (B), 40 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 14 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 47 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).

TABLE 90

	A	B	C	D	E
$\bar{l}$ mm.	0·83	0·63	0·56	0·76	0·73
(var. l)	(0·073)	(0·0475)	(0·049)	(0·067)	(0·082)
$\bar{w}$ mm.	2·54	1·94	1·33	2·21	1·91
(var. w)	(0·66)	(0·567)	(0·351)	(0·597)	(0·644)
r	0·96	0·951	0·915	0·911	0·936
$\log_e \bar{l}$	−0·2366	−0·5187	−0·6523	−0·3292	−0·3864
(var. $\log_e$ l)	(0·1005)	(0·1133)	(0·145)	(0·1096)	(0·1433)
$\log_e \bar{w}$	0·8837	0·5923	0·1943	0·735	0·566
(var. $\log_e$ w)	(0·097)	(0·1407)	(0·1818)	(0·1159)	(0·1622)
r_e	0·974	0·968	0·9458	0·908	0·94
α	0·9824	1·115	1·12	1·028	1·064
(var. α)	(0·00155)	(0·00412)	(0·00356)	(0·02318)	(0·00425)

TABLE 90. Statistics of the anterior (l) and lateral (w) extension of the socket ridges or brachiophores from the dorsal umbo in 34 specimens of *Sowerbyella sericea* (J. de C. Sowerby) (A), 21 of *S. soudleyensis* Jones (B), 39 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 10 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 33 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).

One of the most interesting aspects of the variability within the samples is the evidence presented in Table 92, that all Welsh stocks are more finely costellate than the Shropshire ones : and when exact probability tests are conducted for frequencies in cells of 6–8 and 9 or more costellae per mm., the differences are significant ($p < \cdot 01$). It is tempting to correlate this difference with the finer sediments entombing the Bala shells but this remains to be demonstrated in other *Sowerbyella*. Certainly, phenotypic variation does not seem to have affected the development of rugae (Table 91) because although 4 pairs are most commonly developed in the new subspecies compared with 3 pairs in the other forms, the modes are not pronounced and there is almost complete overlap between all samples. Moreover the wavelengths are similar, ranging from 0·2 to 0·5 mm. but with modal estimates of 0·3 mm. in all 5 samples. In a like manner the change in the cardinal angles due to a decrease in the lateral expansion of the hinge-lines in later growth stages followed the same pattern. Thus taking *S. sericea* as an example the cardinal angles of shells less than 5 mm. long were mostly acute ; but in longer shells the frequencies for acute, rectangular and obtuse angles were 7, 10 and 2.

TABLE 91

	0	1	2	3	4	5	6	7	8
A . .	9	—	6	12	17	1	3	1	—
B . .	2	—	2	5	2	—	—	—	1
C . .	9	2	13	15	11	5	1	—	—
D . .	1	1	—	5	6	1	1	—	1
E . .	3	2	2	5	7	6	1	—	—

TABLE 91. The frequencies of pedicle valves bearing the number of pairs of rugae given in the top row for *Sowerbyella sericea* (J. de C. Sowerby) (A), *S. soudleyensis* Jones (B), *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).

TABLE 92

	6	7	8	9	10	11	12
A . .	3	24	20	6	—	—	—
B . .	—	4	10	4	—	—	—
C . .	—	—	—	2	6	4	2
D . .	—	3	10	10	5	2	—
E . .	—	3	12	15	9	5	1

TABLE 92. The frequencies of brachial valves bearing the counts of costellae per mm. identified in the top row at a distance of 10 mm. antero-medianly of the dorsal umbo for *Sowerbyella sericea* (J. de C. Sowerby) (A), *S. soudleyensis* Jones (B), *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), *S. sericea permixta* from the Lower Allt Ddu Group (D) and *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).

There was also a tendency for the pedicle valves to develop a narrow, rounded to sharp-crested, median fold (subcarina) or, very rarely, a slight median depression (uniplica). The number of pedicle valves, over 5 mm. long, with a subcarinate, unmodified or uniplicate profile respectively is as follows :

13, 40 and 0 for *S. sericea*
34, 12 and 0 for *S. soudleyensis*
2, 7 and 2 for *S. musculosa*
14, 18 and 0 for *S. sericea permixta* from the Lower Allt Ddu
and 7, 26 and 2 for *S. sericea permixta* from the Upper Glyn Gower and Nant Hir Groups. *S. soudleyensis* is clearly distinct from all other samples in the commonness of the subcarinate condition.

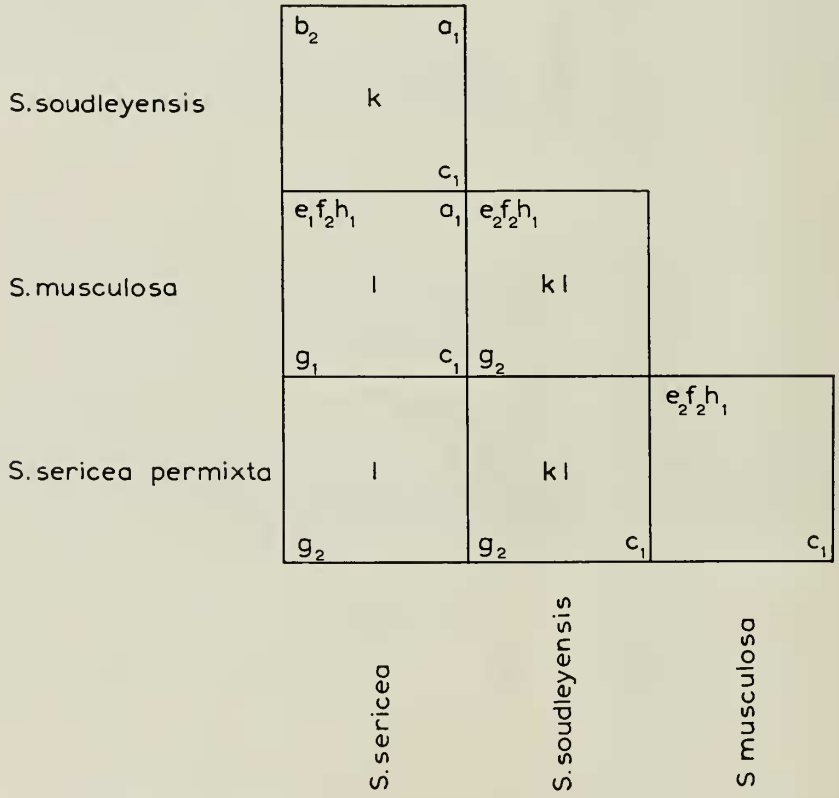

FIG. 12. The distribution of significant differences between any two named species of *Sowerbyella* where a and b respectively represent the relative width and depth of the pedicle valve, c the relative length of the ventral septum, e the relative width of the ventral muscle scar, f and g respectively the relative length and width of the cardinalia, h the relative length of the dorsal submedian septa, i the ventral median fold and l the incidence of costellae per mm.: lower case figures 1 or 2 respectively indicate significant differences in growth rate or inherent shape.

Nine bivariate estimates of relative growth have been calculated for all five samples. They are indices of the outline and profile of the pedicle valve, the outline and relative length of the ventral muscle scar as well as the relative length of the ventral median septum, the relative length and width of the cardinalia, the relative length of the dorsal submedian septa and the relative width of the elevated, tuberculate areas, disposed as a pair of arcs on either side of the submedian septa, which almost certainly gave support to a schizolophous lophophore in *Sowerbyella* ; the relevant statistics are given in Tables 82–90. The samples from the Lower Allt Ddu and the Upper Glyn Gower and Nant Hir Groups did not differ from each other in any aspect of relative growth and in view of other morphological comparisons they may be taken as samples drawn from the same population. Consequently the older, larger sample alone was used for the definition of the new subspecies and was employed in this capacity for comparisons with other stocks.

In all, 20 out of 42 tests of significance showed important differences (p varying from ·05 to ·001) between any two samples either in the growth ratio (a or α) of two attributes or in indices of inherent or residual shape (b or β). The inter-relationships are complicated but when the results are assembled in a matrix table as in Text-fig. 12, the distinguishing features of the various taxa are soon appreciated. Hence, apart from the significantly finer radial ornamentation of the new species and subspecies and the dominantly subcarinate aspect of the pedicle valves of *S. soudleyensis*, it can be seen that :

(1) *S. musculosa* is unique in the inherently greater length relative to width of the ventral muscle field ; the inherently longer socket ridges relative to the length of the brachial valve and in the relatively slower anterior extension of the submedian septa in the brachial valve.

(2) *S. musculosa* and *S. soudleyensis* differ from *S. sericea* (*s.l.*) in the relatively faster forward growth of the ventral septum and from *S. sericea* (*s.s.*) in the faster growth in length relative to width of their pedicle valves.

(3) *S. musculosa* and *S. sericea permixta* differ from *S. sericea* and *S. soudleyensis* in their socket ridges being inherently longer relative to their width.

(4) *S. soudleyensis* differs from *S. sericea* in the inherently greater depth of the pedicle valve relative to length.

It may be premature to derive any conclusions on the evolution of south British *Sowerbyella* from these comparisons but bearing in mind the stratigraphical context of the various stocks, it is probably significant that *S. sericea permixta* is the oldest and also the most generalized form. The new subspecies, for example, is a suitable ancestor for both *S. soudleyensis* and *S. sericea* but, although it is morphologically closer to the latter species, the former is more likely to be its contemporary. Furthermore, *S. musculosa* is decisively distinct from all other stocks in at least the three same features so that even if, on balance, it is morphologically nearer to the new subspecies, it is most probably an intrusive element appearing briefly within the faunal assemblages of the Anglo-Welsh basin. In view of these anomalies therefore, it is unlikely that the Caradocian forms of *Sowerbyella* present a simple picture of direct descent.

Genus *EOPLECTODONTA* Kozlowski 1929

TYPE SPECIES. *Sowerbyella praecursor* Jones by original designation of Kozlowsk (1929 : 112).

Eoplectodonta cf. *rhombica* (M'Coy)

(Pl. 12, figs. 9–14, 18, 19)

1852 *Leptaena sericea* var. *rhombica* M'Coy : 239.
1928 *Sowerbyella rhombica* (M'Coy) Jones : 426–430, pl. 22, fig. 1.

DIAGNOSIS. Semi-circular to subquadrate *Eoplectodonta* with evenly concavo-convex longitudinal profile, rectimarginate or rarely faintly paraplicate anterior commissure and slightly acute to slightly obtuse cardinal angles in adult shells, pedicle valve about one-half as long as wide and over one-third as deep as long ; radial ornamentation consisting of unequally developed parvicostellae segregated into sectors about 1 mm. wide and with counts of 8 to 10 costellae per mm., 10 mm. antero-medianly of ventral umbo, postero-lateral areas, also ornamented by rugae, with wavelength of over 0·25 mm. disposed acutely to hinge-line and commonly forming 10 or 11 pairs extending antero-medianly through sectors of up to 30°; pseudodeltidium and chilidium small, apical ; teeth elongate, divergent dental lamellae obsolescent, denticles, about 3 to 4 per mm. commonly developed for over one-half the length of hinge-line lateral to teeth, but rarely throughout entire length ; ventral muscle field divided and deeply cordate in outline about three-quarters as long as wide and extending anteriorly for about one-half the length of pedicle valve, adductor scars small lanceolate, separated by median septum extending anteriorly for over one-half the length of field and deeply inserted posteriorly into callist beneath pseudodeltidium, diductor scars widely separated anteriorly and divided by divergent *vascula media* giving rise to lemniscate pallial sinus pattern ; cardinalia more than one-third as long as wide and consisting of strong high median cardinal process protruding ventrally of hollowed notothyrial platform and fused with chilidial plates and widely divergent socket ridges, median ridge strong and high, arising later than submedian septa but becoming ankylosed with them in adult valves, septa extending anteriorly for nearly three-fifths the length of brachial valve and flanked by pair of subpetaloid, elevated " lophophore platforms " divided by *vascula myaria* and about seven-tenths as long as wide ; pallial sinus pattern lemniscate.

MATERIAL (Figured).	length	width (mm.)
Internal mould of pedicle valve (BB.29122)	13·5	22·0
Incomplete internal mould of pedicle valve (BB.29123)	9·0	—
Deformed external mould of pedicle valve (BB.29125)	9·0	15·5
Incomplete external mould of pedicle valve (BB.29126)	—	—

Material (Figured) (*continued*).	length	width (mm.)
Deformed external mould of brachial valve (BB.29127)	8·0	—
Incomplete internal mould of brachial valve (BB.29128)	11·5	—
Deformed internal mould of brachial valve (BB.29129)	8·0	—
Deformed internal mould of brachial valve (BB.29130)	—	—

Horizon and localities. Gelli-grîn Group : BB.29122, BB.29128, BB.29130 from calcareous ashes exposed at the south edge of wood, 850 ft. west of Gelli-grîn Farm ; BB.29126–27 from calcareous ashes along the north side of track leading west from Gelli-grîn Farm and 1,000 ft. west-south-west of the farm ; BB.29123, BB.29125, BB.29129, from calcareous ash quarry beside the drive to Y Garnedd Farm.

Discussion. The complications that arise in restricting M'Coy's specific name *Eoplectodonta rhombica* to fossils from one locality have been adequately dealt with by Jones (1928 : 426–430) and do not require reiteration. Indeed, as a result of his investigations, the lectotype for the species is now a poorly preserved pedicle valve from the " Bala Limestone of Horton in Ribblesdale " (Jones 1928 : 427). According to King & Wilcockson (1934 : 11) the specimen was collected from the Crag Hill Beds which are now believed to be low Ashgillian in age (King & Williams 1948 : 207) an opinion confirmed by Dr. W. T. Dean in correspondence. Unfortunately, no good collection of topotypic material of *E. rhombica* was available for examination by the writer. But a few moulds of an *Eoplectodonta* from the *Calymene* Beds of Sally Beck, which is probably conspecific with *E. rhombica* (*s.s.*), showed no important differences from the Bala sample, except possibly for being relatively longer and less rugate. These differences, however, cannot at present be employed to distinguish between the two stocks because some of the Bala shells are similar to the Ashgillian moulds in outline and the suppression of rugation, and until we are in a position to assess the variability of both forms they must be considered conspecific irrespective of the difference in age.

As far as the Welsh shells are concerned, most of the relevant data are given in the diagnosis and in Tables 93–96. The pedicle valves are generally evenly convex, with only a faint paraplication antero-medianly in 7 out of 20 valves, and a mean percentage depth relative to length of 37·3 (variance 113·73) in 9 pedicle valves between 4 and 12·5 mm. long. The parvicostellate radial ornamentation is rather finely developed with counts of 6, 7, 8, 9, 10 and 11 costellae per mm., 10 mm. antero-medianly of the umbones of 1, 4, 14, 34, 15 and 5 pedicle valves ; at this distance from the ventral umbo thickened costellae divide the pattern into well defined segments with an average width of 1·0 mm. (variance 0·042) in 39 specimens. The rugae are also characteristic. They occupy up to 30° sectors in the postero-lateral areas in an interrupted concentric pattern which begins at 1 to 2 mm. from

the umbo and subtends acute angles with the hinge-line. For 31 specimens the average wavelength was 0·27 mm. (variance 0·0015) and 9, 10, 11, 12, 13, 14 and 15 rugae were counted along the right hinge lines of 2, 4, 3, 4, 1, 2 and 1 pedicle valves.

Internally the most interesting feature is the development of the triseptate condition of the brachial valve because like the American and Scottish species (see Williams 1962 : 184) the median ridge develops after the submedian septa that form the inner boundaries to the lophophore platform. In 7 out of 9 of the smallest brachial valves, with the submedian septa up to 2·9 mm. long, the median ridge is seen to have developed later than the diverging submedian septa ; in the remaining 2 specimens no ridge occurred. This condition persisted in some specimens so that the ridge was also absent in 4 out of 12 specimens with submedian septa up to 5·9 mm. long. But in 2 out of 8 specimens with longer submedian septa, excessive secretion of secondary shell about the ridge caused it to fuse posteriorly with the notothyrial platform and so to dominate the median region of the valve as an eminence raised above the level of the submedian septa.

TABLE 93

$\bar{l}$ mm. (var. l)	6·1	(5·868)
$\bar{w}$ mm. (var. w)	12·1	(23·407)
r	0·966	
a (var. a)	1·997	(0·01025)

TABLE 93. Statistics of length (l) and maximum width (w) of 28 pedicle valves of *Eoplectodonta* cf. *rhombica* (M'Coy).

TABLE 94

$\bar{l}$ mm. (var. l)	7·5	(7·719)
$\bar{sc}$ mm. (var. sc)	3·8	(2·352)
r	0·832	
a (var. a)	0·552	(0·00446)

TABLE 94. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for 23 specimens of *Eoplectodonta* cf. *rhombica* (M'Coy).

TABLE 95

$\bar{l}$ mm. (var. l)	3·3	(1·409)
$\bar{w}$ mm. (var. w)	4·3	(1·405)
r	0·903	
$\log_e \bar{l}$ (var. $\log_e$ l)	1·1228	(0·1239)
$\log_e \bar{w}$ (var. $\log_e$ w)	1·4168	(0·0744)
r_e	0·910	
α (var. α)	0·7749	(0·00685)

TABLE 95. Statistics of length (l) and maximum width (w) of the ventral muscle scar of 17 pedicle valves of *Eoplectodonta* cf. *rhombica* (M'Coy).

Table 96

$\bar{l}$ mm. (var. l)	6·4	(6·57)
$\bar{s}$ mm. (var. s)	3·8	(2·216)
r	0·927	
a (var. a)	0·5808	(0·00237)

Table 96. Statistics of length of brachial valve (l) and length of submedian septa (s) for 22 specimens of *Eoplectodonta* cf. *rhombica* (M'Coy).

Between 8 and 21 denticles occurred along the right hinge-lines of 14 specimens but in only one valve did denticles occupy the entire hinge-line ; mostly they occupied between one-third and three-quarters of the hinge-line with an average of just over one-half for 7 specimens.

E. cf. *rhombica* is clearly quite distinct from *E. acuminata* (Holtedahl 1916) emended Spjeldnaes (1956 : 96), *E. semirugata* (Reed 1917) emended Williams (1962 : 181) and *E. lenis* Williams (*In* Whittington & Williams 1955 : 417) at least in the much greater concavo-convexity of its profile. At the same time it is different from *E. conspicua* (Reed 1917) emended Williams (1962 : 182), to which it has frequently been compared (Jones 1928 : 431), in lacking the carination of the pedicle valve and in having a significantly greater relative width due to the faster anterior growth of the Scottish shells.

Genus ***SERICOIDEA*** Lindström 1953

Type species. *Leptaena sericea* var. *restricta* Hadding by original designation of Lindström (1953 : 134).

Sericoidea sp.

(Pl. 12, figs. 15, 16)

A small number of poorly preserved *Sericoidea* have been collected from calcareous ashes of the Gelli-grîn Group exposed above the Limestone in the old quarries in Ffridd Bach, south of Maes-meillion Farm, and the casts of incomplete moulds of a dorsal interior (BB.29155) and a ventral exterior (BB.29156) have been figured to illustrate the chief characteristics of the species.

The shells were evidently gently concavo-convex in profile and semi-circular in outline and were ornamented by fine parvicostellae segregated into narrow segments by a thickening of every fifth or sixth costella and numbering about 12 per mm. at 2 mm. antero-medianly of the ventral umbo. No interior of the pedicle valve is well enough preserved to show more than the obsolescence of the dental lamellae but the dorsal interior is sufficiently distinctive to indicate that the stock is quite different from other described species attributed to the genus. Thus, although the cardinalia were orthodoxly arranged with a high median cardinal process and a pair of widely divergent socket ridges, a well defined lophophore platform was built up in adult valves by the amalgamation of relatively long septa. The septa themselves, up to 17 in number, consisted of a strong median one, extending forward for about three-fifths the length of the valve, flanked by two sets of smaller ones

disposed in a pair of arcs. Each septum was highest and thickest at its anterior end and tended to fuse with its neighbours posteriorly so that a platform, deeply indented medianly and sharply crenulated peripherally, resulted.

The elaboration of a lophophore platform by the lateral fusion of a number of septa serves to distinguish the Gelli-grîn *Sericoidea* from *S. abdita* Williams which is known to occur in the Nant Hir Group (Whittington & Williams 1955 : 418). For in adult brachial valves of the latter species the median septum is flanked by only 3 pairs of discrete short septa arranged in arc. Even in the more advanced *S. restricta* (Hadding) from the Sulårp Shale of Sweden and the Craighead Limestones and Mudstones of Scotland (see Williams 1962 : 187–190), the arc defining the anterior of the lophophore platform consists of discrete septules and there is little doubt that the Gelli-grîn forms will prove to be specifically distinct when enough material is obtained to assess the variability of their morphology.

Superfamily STROPHOMENACEA King 1846

Family STROPHOMENIDAE King 1846

Genus ***STROPHOMENA*** de Blainville 1825

Type species. *Strophomena rugosa* Rafinesque by subsequent designation of King (1846 : 28).

Strophomena grandis (J. de C. Sowerby)
(Pl. 12, figs. 17, 20, 21 ; Pl. 13, fig. 2)

1839 *Orthis grandis* J. de C. Sowerby : 638, pl. 20, figs. 12, 13.
1933 *Longvillia grandis* (J. de C. Sowerby) Bancroft : 3.

Diagnosis (emended). Elongately semi-oval, gently convexo-concave *Strophomena* with pedicle valve about seven-tenths as long as wide slightly convex for about 3 mm. around the umbonal region but slightly and evenly concave in transverse and longitudinal profiles of adult valves, brachial valves about one-eighth as deep as long, cardinal angles slightly acute to rectangular, ventral interarea apsacline, pseudodeltidium small, foramen sealed at least in adult valves, dorsal interarea anacline, chilidium arched and only covering the dorsal ends of cardinal process lobes ; radial ornamentation strongly unequally parvicostellate with 4 costellae per mm., 10 mm. antero-medianly of ventral umbo and commonly with every third or fourth thickened to give narrow segments ; teeth small, obliquely disposed and fused with short dental lamellae subtending an angle of about 90° at apex, ventral muscle field commonly faintly impressed especially anteriorly, over two-fifths as long as pedicle valve and tending to be subcircular in young valves, but longer than wide in adult shells with submedian diductor lobes extending well beyond anterior limits of lanceolate adductor scar but not completely enclosing it ; ventral pallial sinus pattern probably digitate, *vascula media* subparallel dividing anteriorly ; cardinal process lobes, long, divergent with deeply concave posterior faces and ankylosed to widely divergent socket ridges, notothyrial platform

and median ridge faintly developed, dorsal adductor scars lightly impressed, obscure anteriorly but probably subtriangular and divided by at least two pairs of low divergent ridges ; dorsal pallial sinus pattern unknown.

		length	width (mm.)
LECTOTYPE.	Internal mould of pedicle valve (G.S.M., Geol. Soc. Coll. 6823)	38·0	48·0
OTHER MATERIAL	Internal mould of brachial valve (G.S.M. Geol. Soc. Coll. 6897),	36·0	—
	Incomplete external mould of pedicle valve (BB.29150)	30·0	—
	Incomplete external mould of brachial valve (BB.29151)	—	—

HORIZON AND LOCALITIES. Marshbrookian Stage : G.S.M., G.S.C. 6823, G.S.M., G.S.C. 6897 from " Acton Scott "; BB.29150–51 from buff coloured sandstones exposed in the quarry in Marsh Wood.

DISCUSSION. It is clear from the fossils associated with the specimens described by Sowerby as *Orthis grandis* that they were originally taken from the *Dalmanella wattsi* beds of South Shropshire and, in redefining the species, only moulds recovered from this horizon have been used. Complete specimens are, however, comparatively rare so that not very much information on the variability of the stock can be provided. The shell is transversely semi-oval in outline with the greatest width at the hinge-line although a mucronate condition is unknown at least in adult stages of growth. The mean percentage length relative to width (with variance) for five pedicle valves between 10 and 30 mm. long was 71·6 (17·25). The radial ornamentation is typically strophomenid with counts of 4 costellae per mm. in six pedicle valves at a distance of 10 mm. antero-medianly of the umbo. The lectotype (G.S.C. 6823) is an internal mould of a gerontic pedicle valve in which the ventral muscle field is exceptionally well defined and is elongately suboval in outline being about three-quarters as wide as long. In smaller pedicle valves, the anterior boundaries to the ventral muscle field are obscure and even when they are well seen, as in two valves 26 and 29 mm. long, they are subcircular in outline and about as wide as long. The accelerated anterior migration of the muscle field in late growth stages, however, must have been concomitant with a greater anterior growth of the shell, because in the lectotype and the two valves just mentioned the percentage length of the fields relative to that of the valves was 42, 44 and 44 respectively.

Bancroft (1933 : 3) proposed the genus *Longvillia* with *Strophomena grandis* as type species. In so doing he compared the genus with *Fardenia* Lamont, but made no reference at all to *Strophomena*. The omission is a curious one, unless he believed the " *pecten*-group " of shells to typify *Strophomena* because *S. grandis* is in no way generically separable from *S. planumbona* Hall and other typical members of that genus.

Strophomena sp.
(Pl. 13, figs. 1,3,4)

Incomplete external and internal moulds of a pedicle valve (BB.29062–63) recovered from sandstones of the Upper Allt Ddu Group exposed on the western side of Bryn Cut, about 50 ft. below the Pont-y-Ceunant Ash and 650 ft. east of Holy Trinity Church ; and an internal mould of a brachial valve (BB.28887) collected from calcareous ashes of the Gelli-grîn Group cropping out above the Gelli-grîn Limestone in the old quarries at Ffridd Bach, south of Maes-meillion have been figured to show the *Strophomena* that very rarely occurs in the highest Caradocian rocks of the Bala district. The pedicle valve, about 23 mm. long, was transversely semi-oval in outline with acute cardinal angles and evenly concave transverse and longitudinal profiles attaining a maximum depth of about one-sixth the length of the valve. The radial ornamentation was unequally parvicostellate with finely cancellated, closely packed, rounded costellae numbering 6 per mm., at 10 mm. antero-medianly of the ventral umbo ; the interarea was apsacline, the pseudodeltidium well developed and the foramen small and supra-apical. Internally, the small teeth were supported by divergent dental lamellae extending anteriorly for about one-sixth the valve length ; and the subflabellate ventral muscle field was slightly wider than long and over two-fifths as long as the valve with a well developed, lanceolate and undifferentiated adductor scar, located postero-medianly and enclosed by the lobate diductor scars. A conspicuous subperipheral rim of secondary shell, indented by pallial sinus furrows, occurred within 3–4 mm. of the valve margin.

The dorsal mould shows that the brachial valve which was about 17 mm. long, was also transversely semi-oval in outline, gently convex in profile, and similarly equipped with a subperipheral rim. The cardinal process lobes were small but conspicuous, ankylosed to a faint median ridge and to the widely divergent socket ridges ; the dorsal adductor scars were only vaguely impressed on either side of the median ridge about two pairs of divergent, low ridges.

The species is clearly related to *Strophomena grandis* J. de C. Sowerby but differs from it, at least in being more highly convexo-concave and more finely ornamented and in the subquadrate outline of the ventral muscle scar. These differences will probably prove to be significant but until more material is obtained to assess the variability of these and other features it is better to withhold taxonomic recognition.

Genus ***GLYPTOMENA*** Cooper 1956

Type species. *Glyptomena sculpturata* Cooper by original designation of Cooper (1956 : 881).

Glyptomena* cf. *osloensis (Spjeldnaes)
(Pl. 13, figs. 5, 6, 8, 9)

Description. Subquadrate, strongly concavo-convex *Glyptomena* ornamented postero-laterally by 3 or 4 pairs of short rugae with a wavelength of about 1 mm.

disposed at a slightly acute angle to the hinge-line and extending forwards through a 35° sector of the shell surface, radial ornamentation consisting of unequal, rounded, parvicostellae well differentiated into segments up to 1·5 mm. thick and numbering about 5 per mm., 10 mm. antero-medianly of the ventral umbo ; pseudodeltidium small or lacking, chilidium large, strongly convex ; teeth large, pustulose, continuous with widely divergent, short dental lamellae, ventral muscle scar subrhomboidal in outline, adductor scars lanceolate, separated by a faint median ridge and about one-half as long as the slightly divergent, submedian diductor lobes ; dorsal interior imperfectly preserved, notothyrial platform short, three-pronged with the lateral extensions fused with wide-splayed socket ridges, adductor impressions contained posteriorly between the median and lateral prongs and divided by a pair of slightly divergent low ridges.

Material (Figured). One internal and two external moulds of pedicle valves (BB.29101–03). Fragment of internal mould of brachial valve (BB.29104).

Horizon and locality. Gelli-grîn Group : all specimens from calcareous ashes immediately west of deep, overgrown quarry, 1,450 ft. east-north-east of Y Garnedd Farm.

Discussion. A few moulds, taken from the Gelli-grîn Group, are evidently representative of the genus *Glyptomena* Cooper (see Williams 1962 : 210) and compare closely with *G. osloensis* (Spjeldnaes 1957 : 161–167) from stage 4bα of Norway. There are, however, some differences, notably the rounded geniculate profile of the Norwegian shells, but this is not greatly different from the very strong convexity of the Welsh specimens and until more is known about the variability of the latter it is feasible to treat the stocks as conspecific.

Genus *MACROCOELIA* Cooper 1956

Type species. *Macrocoelia obesa* Cooper by original designation of Cooper (1956 : 890).

Macrocoelia expansa (J. de C. Sowerby)

(Pl. 13, figs. 7, 10–14 ; Pl. 14, figs. 1, 2, 5 ; Text-fig. 13)

1839 *Strophomena expansa* J. de C. Sowerby : 638, pl. 20, fig. 14.

1871 *Strophomena expansa* Sowerby ; Davidson : 312 *pars*, pl. 45, figs. 1, 6, 8, 10, *non* figs. 2–5, 7, 9.

Diagnosis (emended). Elongately subquadrate to semi-oval, concavo-convex *Macrocoelia* with evenly convex pedicle valve almost four-fifths as long as wide and almost one-eighth as deep as long, cardinal angles slightly obtuse to slightly acute ; radial ornamentation strongly unequally parvicostellate, finely cancellate and tending to curve outwards posterolaterally with counts of 4 or 5 costellae per mm., at 10 mm. anterior of ventral umbo and commonly with every third or fourth

costella thickened to give a narrowly segmented appearance ; 3 to 5 impersistent rugae commonly developed postero-laterally disposed at acute angles to hinge-line and extending antero-medianly through a sector of about 20–25° in each postero-lateral area ; ventral interarea apsacline, delthyrium relatively narrow, pseudo-deltidium absent in adult shells, dorsal interarea anacline, chilidium large and convex; teeth small, elongated and ankylosed with widely divergent dental lamellae to form pair of hollow, acutely triangular structures extending anteriorly for about one-twelfth the length of pedicle valve ; ventral muscle field large, splayed, subcircular extending anteriorly for about one-half the length of pedicle valve and about four-fifths as long as wide with elevated radiating ridges separating each diductor scar into as many as 5 distinct lobes in adult shells, pedicle callist well developed, passing into broad, medianly indented ridge extending anteriorly for about one-seventh the length of pedicle valve, adductor scars lanceolate, commonly indistinct and impressed anterior of ridge ; cardinal process lobes with splayed posterior faces, not greatly elevated above anchor-shaped notothyrial platform, median septum between lobes commonly vestigial ; socket ridges elongate and ankylosed to lateral extensions of notothyrial platform, dorsal adductor impressions vague, divided by pair of narrowly divergent ridges ; ventral pallial sinus pattern saccate with up to 4 pairs of arcuate branches arising from subjacent *vascula media* ; dorsal pattern unknown.

Fig. 13. The ventral internal mould of *Macrocoelia expansa* (J. de C. Sowerby), ×2·5 approx., showing the pallial sinus pattern : *gg, vascula genitalia* ; *m, vascula media.*

		length	width (mm.)
Lectotype.	Incomplete internal mould of pedicle valve (G.S.M., Geol. Soc. Coll. 6863)	—	—
Other material.	Incomplete internal mould of brachial valve (BB.29112)	—	—
	Incomplete internal mould of pedicle valve (BB.29113)	—	—
	External mould of pedicle valve (BB.29114)	17·0	—
	Internal mould of pedicle valve (BB.29115)	37·0	43·0
	Internal mould of pedicle valve (BB.29116)	17·0	22·0
	Incomplete internal mould of brachial valve (BB.29117)	—	—
	External mould of pedicle valve (BB.29118)	39·0	46·0
	External mould of pedicle valve (BB.29119)	—	—

Horizon and locality. Lower Longvillian Substage : lectotype G.S.M., G.S.C. 6863 from " Caradoc Sandstone, Meifod ", Montgomeryshire ; all other specimens from siltstones exposed on Gallt-yr-ancr, 440 yds. north of west from Dyffryn, one-half mile south-west of Meifod Church.

Macrocoelia prolata sp. nov.

(Pl. 14, figs. 3, 4, 6–10)

Diagnosis. Elongately semi-oval, concavo-convex *Macrocoelia* with evenly convex pedicle valve over four-fifths as long as wide and less than one-fifth as deep as long, cardinal angles slightly obtuse to slightly acute ; radial ornamentation strongly unequally parvicostellate, finely cancellate and curving outwards postero-laterally, with counts of 6 or 7 costellae per mm., at 10 mm. anterior of ventral umbo and commonly with every third or fourth costella thickened to give a narrowly segmented appearance ; about 8 impersistent rugae developed postero-laterally, disposed at acute angles to hinge-line and extending antero-medianly through a sector of about 45° in each postero-lateral area ; ventral interarea apsacline, delthyrium relatively narrow, pseudodeltidium absent in adult shells, dorsal interarea anacline, chilidium large and convex ; teeth small, elongated and ankylosed with widely divergent dental lamellae to form pair of hollow acutely triangular structures extending anteriorly for about one-tenth the length of pedicle valve ; ventral muscle field large, splayed, subcircular in outline, extending anteriorly for less than one-half the length of pedicle valve and about nine-tenths as long as wide with elevated radiating ridges separating each diductor scar into as many as 5 distinct

lobes in adult shells, pedicle callist well developed, passing into broad, medianly indented ridge extending anteriorly for about one-seventh the length of pedicle valve, adductor scars indistinct ; posterior faces of cardinal process lobes not greatly splayed or elevated above anchor-shaped notothyrial platform, median septum between lobes commonly vestigial ; socket ridges elongate and ankylosed to lateral extensions of notothyrial platform, dorsal adductor scars vaguely impressed and divided by pair of narrowly divergent ridges ; pallial sinus patterns unknown.

		length	width (mm.)
Holotype.	External mould of pedicle valve (BB.29106)	—	25·0
Paratypes.	External mould of pedicle valve (BB.29107)	9·5	12·5
	External mould of pedicle valve (BB.29105)	16·5	20·0
	Internal mould of pedicle valve (BB.29108)	10·0	11·5
	Incomplete internal mould of pedicle valve (BB.29109)	—	—
	Incomplete internal mould of brachial valve (BB.29110)	—	—
	Incomplete internal mould of brachial valve (BB.29111)	—	—

Horizon and locality. Allt Ddu Group : BB.29105 from crags of fine sandstones and mudstones, 1,100 ft. south-west of Eglwys Anne ; BB.29106–11 from fine sandstones underlying the Pont-y-Ceunant Ash and exposed north of the drive to Y Garnedd Farm.

Discussion. The species *Strophomena expansa* J. de C. Sowerby is a well known but inadequately defined stock that has been widely identified in Caradocian rocks from a number of localities throughout Britain (see Davidson 1871 : 314). There is, however, no doubt that when Sowerby erected the species, he had in mind the strophomenids occurring abundantly and in association with *Howellites antiquior* (M'Coy) in fine, blue-grey sandstones exposed in the vicinity of Meifod (see Whittington 1938 : 428–431). Accordingly, a good sample, taken from exposures on Gallt-yr-ancr, has been used to provide a revised description of the species which is also now recognised as belonging to the genus *Macrocoelia*.

Macrocoelia also occurs sporadically in the Allt Ddu Group of the Bala district. It is commonest in the ashy sandstone members towards the top of the formation and, although related to *M. expansa*, a sample from this horizon has proved to be distinct in a sufficient number of features to merit taxonomic recognition. In shell outline and profile (Tables 97, 100) there is no important difference between the two species because although the pedicle valves of the new species tend, on an average, to be relatively longer and deeper the discrepancies are covered by the variability of the samples. The surface ornamentation of the new species however, is quite

distinctive. Counts of 3, 4, 5, 6, 7 and 8 costellae per mm. at a distance 10 mm. antero-medianly of the ventral umbo, were obtained in 0, 0, 0, 4, 9 and 2 pedicle valves of the new species compared with 5, 10, 15, 6, 1 and 0 valves of *M. expansa* ; the differences are highly significant ($p < \cdot001$). In both species, rugae with a wavelength of 0·5 mm. are disposed at acute angles to the hinge-line but they are longer in the new species extending antero-medianly through 45° sectors of the postero-lateral areas compared with 20–25° sectors in *M. expansa*. The rugae are also more numerous and persistent in the new species because they have been seen on every external mould examined and 7, 8, 9 and 10 have been counted on the right sides of 1, 5, 2 and 2 pedicle valves compared with 2, 3, 4, 5, 6, 7 and 8 on the right sides of 2, 10, 7, 6, 1, 5 and 3 pedicle valves of *M. expansa* with no rugae developed at all in a further 15 valves.

TABLE 97

	A	B
$\bar{l}$ mm. (var. l)	22·9 (123·987)	10·2 (29·853)
$\bar{w}$ mm. (var. w)	28·9 (189·979)	12·0 (34·304)
r	0·989	0·993
$\log_e \bar{l}$ (var. $\log_e$ l)	3·0248 (0·2126)	2·1917 (0·2533)
$\log_e \bar{w}$ (var. $\log_e$ w)	3·2618 (0·2053)	2·3765 (0·2167)
r_e	0·987	0·993
α (var. α)	0·9827 (0·00113)	0·925 (0·0008)

TABLE 97. Statistics of length (l) and maximum width (w) of 24 pedicle valves of *Macrocoelia expansa* (J. de C. Sowerby) (A) and of 17 pedicle valves of *M. prolata* sp. nov. (B).

TABLE 98

	A	B
$\bar{l}$ mm. (var. l)	28·7 (66·131)	23·5 (75·625)
$\bar{sc}$ mm. (var. sc)	14·6 (19·933)	11·4 (30·519)
r	0·958	0·974
$\log_e \bar{l}$ (var. $\log_e$ l)	3·2779 (0·078)	3·0928 (0·1283)
$\log_e \bar{sc}$ (var. $\log_e$ sc)	2·6353 (0·09)	2·3243 (0·2118)
r_e	0·954	0·984
a (var. a)	1·074 (0·00334)	1·285 (0·00748)

TABLE 98. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for 33 specimens of *Macrocoelia expansa* (J. de C. Sowerby) (A) and for 9 specimens of *M. prolata* sp. nov. (B).

TABLE 99

	A	B
$\bar{l}$ mm. (var. l)	15·3 (14·893)	10·6 (12·77)
$\bar{w}$ mm. (var. w)	18·2 (22·063)	11·4 (16·968)
r	0·934	0·997
a (var. a)	1·217 (0·0051)	1·153 (0·00159)

TABLE 99. Statistics of length (l) and maximum width (w) of the ventral muscle scars of 39 pedicle valves of *Macrocoelia expansa* (J. de C. Sowerby) (A) and of 7 pedicle valves of *M. prolata* sp. nov. (B).

TABLE 100

$\bar{l}$ mm. (var. l) . .	11·6	(37·445)
$\bar{th}$ mm. (var. th) . .	2·1	(1·379)
r . . .	0·946	
a (var. a) . . .	0·1919	(0·00035)

TABLE 100. Statistics of length (l) and maximum depth (th) of 13 pedicle valves of *Macrocoelia prolata* sp. nov.

The only known internal differences relate to the relative length of the ventral muscle scars. In both species the muscle scars are subcircular and splayed and only slightly wider than long (Table 99) with well developed postero-median ridges. The ridges have a mean percentage length relative to the length of 9 pedicle valves of *M. expansa*, between 18 and 37 mm. long, of 13·5 (variance 3·095) compared with 14·1 for 3 pedicle valves of *M. prolata*. There is however an important difference in the anterior advance of the ventral muscle field because although the scars of the Bala species were, on an average, only slightly shorter, relative to the length of the pedicle valves, than those of *M. expansa*, they were inherently so ; and a comparison of the growth rates, (Table 98), shows that the scars of the new species expanded anteriorly at a significantly faster rate ($p < ·05$).

In summary then, the new species differs from *M. expansa* in its finer radial ornamentation, in the invariable presence of more numerous and longer rugae and in the relatively faster anterior migration of the ventral muscle scar : and in respect of these features other, rarer *Macrocoelia* collected from older rocks in the Bala district are clearly related to *M. prolata* rather than *M. expansa*.

Genus ***HEDSTROEMINA*** Bancroft 1929

TYPE SPECIES. *Hedstroemina fragilis* Bancroft by original designation of Bancroft (1929 : 56).

Hedstroemina ? spp.

(Pl. 14, figs. 11, 12)

Two internal ventral moulds (BB.29120–21) of a rafinesquinid stock have been collected respectively from siltstones of the Glyn Gower Group exposed as crags in the wood immediately east of Cefn-bodig and from mudstones of the Nant Hir Group cropping out on the left bank of the Nant Hir, 600 ft. north-east of Cefn-y-maes Farm and are the only specimens known from the post-Derfel Limestone rocks of the Bala district that can be referred to either *Kjaerina* Bancroft (1929) or *Hedstroemina* Bancroft (1929). The mould from the Glyn Gower rocks (BB.29120) is of an elongately oval, evenly convex pedicle valve, about 11 mm. long and over one-quarter as deep as long with small, thin, divergent dental lamellae extending anteriorly for less than one-tenth the length of the valve. The muscle field appears to have been small but the impressions are indistinct ; the radial ornamentation is impressed towards the margin and shows that the pattern was an unequally parvicostellate one with about 7 costellae per mm., at 10 mm. antero-medianly of the umbo.

The other mould (BB.29121), which is 12 mm. long, is quite different in outline and profile for it represents a transversely oval pedicle valve about three-quarters as long as wide and less than one-fifth as deep as long, although it, too, is characterized by fragile, moderately divergent dental lamellae, obscure muscle impressions and peripherally impressed, unequally developed parvicostellae with about 6 costellae per mm. antero-medianly.

It is possible that these two specimens represent two distinct species but at present even their generic identification is in doubt. Thus the Nant Hir specimen is reminiscent of *Hedstroemina parva* (Bancroft 1929 : 57, pl. 2, fig. 5) whereas the Glyn Gower mould is very like *Kjaerina horderleyensis* (Bancroft 1929 : 50, pl. 1, fig. 12) a form that lacks the strong median rib so typical of *Kjaerina*. Indeed it is only the absence of this feature that has prompted the provisional allocation of both specimens to *Hedstroemina* ; more material might show the stocks to be *Kjaerina* which is characterized by equally generalized ventral internal features.

Family LEPTAENIDAE Cooper 1956

Genus *LEPTAENA* Dalman 1828

Type species. *Leptaena rugosa* Dalman by subsequent designation of King (1846 : 28).

Leptaena salopiensis sp. nov.

(Pl. 15, figs. 7, 8, 10–16)

Diagnosis. Concavo-convex, strongly geniculate *Leptaena* with disc surrounded by prominent, ventral fold with wavelength of 2–3 mm. and complementary dorsal trench, disc transversely quadrate, about 13 mm. long, just over three-fifths as long as wide and with ventral depth of about one-sixth the length due to strongly convex ventral umbo, trail bent back sharply at about 100° to give an overall depth of about two-fifths the length of adult pedicle valves ; radial ornamentation parvicostellate and not well differentiated into segments, commonly with 4 rounded costellae per mm., 10 mm. antero-medianly of ventral umbo ; 5 or 6 concentric and rarely discontinuous rugae, with wavelength of about 1·5 mm. in later ones also ornament the disc ; pseudodeltidium small, foramen small, commonly sealed in adult shells, chilidium large, convex and commonly bearing slight median depression ; teeth obliquely splayed and fused with widely divergent short dental lamellae, ventral muscle scar elongately rhomboidal in outline, nearly nine-tenths as wide as long and extending anteriorly for nearly three-quarters the length of disc in adult shells, adductor scars small, lanceolate separated posteriorly by low median ridge extending from low median platform occupying delthyrial floor, submedian diductor lobes extending well beyond adductors but not enclosing them ; cardinal process lobes slender and commonly separated by faint median ridge, notothyrial platform anchor-shaped with short median stem and strongly curved lateral ridges fused with socket ridges and enclosing posteriorly the subcircular adductor impressions ; a pair of curved submedian ridges originate near median prolongation of notothyrial platform to divide adductor impressions and converge anteriorly commonly to contain anterior median ridge.

		length	width (mm.)
Holotype.	External and internal mould of pedicle valve (BB.29144–45)	20·0	29·0
Paratypes.	External and internal moulds of pedicle valve (BB.29136–37)	16·0	25·0
	External and internal moulds of pedicle valve (BB.29138–39)	17·0	31·0
	External and internal moulds of brachial valve (BB.29140–41)	13·0	—
	Incomplete external and internal moulds of brachial valve (BB.29142–43)	—	—

Horizon and locality. Actonian Stage : all specimens from loose blocks near Acton Scott Church, possibly from the quarry of Castle Hill, one-third of a mile west-south-west of Acton Scott.

Leptaena ventricosa sp. nov.

(Pl. 15, figs. 1–6, 9)

Diagnosis. Concavo-convex, strongly geniculate *Leptaena* with disc surrounded by prominent fold with wavelength of 2–3 mm., disc transversely quadrate, about 9 mm. long, just over three-fifths as long as wide and with ventral depth of about one-fifth the length due to strongly convex ventral umbo, trail bent back sharply at about 90° to give an overall depth of about one-half the length of pedicle valve ; radial ornamentation parvicostellate and not well differentiated into segments, commonly with 4 rounded costellae per mm., 10 mm. antero-medianly of ventral umbo ; 8 or 9 concentric and rarely discontinuous rugae, with wavelength less than 1 mm., in later formed ones also ornament disc ; pseudodeltidium small, foramen small, commonly sealed in adult shells, chilidium large, convex and commonly bearing slight median depression ; teeth large, strongly striated, obliquely splayed and fused with widely divergent short dental lamellae, ventral muscle scar elongately rhomboidal in outline, nearly nine-tenths as wide as long and extending anteriorly for nearly three-quarters the length of disc in adult shells, adductor scars small, lanceolate, separated posteriorly by low median ridge extending from low median platform occupying delthyrial floor, submedian diductor lobes extending well beyond adductors but not enclosing them ; cardinal process lobes well developed, high and separated by faint median ridge, sockets striated, notothyrial platform anchor-shaped with short median stem and strongly curved lateral ridges fused with socket ridges and enclosing posteriorly the subcircular adductor impressions ; a pair of curved submedian ridges originate near median prolongation of notothyrial platform to divide adductor impressions and converge anteriorly commonly to contain anterior median ridge.

		length	width (mm.)
Holotype.	Incomplete external and internal mould of brachial valve (BB.29044–45)	—	—
Paratypes.	External mould of pedicle valve (BB.29042)	10·0	—
	Deformed internal mould of brachial valve (BB.29043)	11·0	—
	Deformed internal mould of pedicle valve (BB.29041)	—	—
	Incomplete internal mould of brachial valve (BB.29046)	—	—
	Deformed internal mould of pedicle valve (BB.29047)	15·0	—
	External mould of pedicle valve (BB.29048)	—	—

Horizon and localities. Gelli-grîn Group : BB.29042, BB.29044–45, from ashy mudstones exposed on the right bank of the Hirnant, 1,200 ft. east-north-east of Ty'n-y-wern Farm ; BB.29041, BB.29047 from calcareous ash crags immediately west of the fence, 1,100 ft. just south of west of Gelli-grîn Farm ; BB.29043 from calcareous ash scarp immediately east of wall and 150 ft. north of sheepfold, 2,600 ft. east of Pont-y-onen Farm ; BB.29046 from calcareous ashes before the Rhiwlas Limestone scarp on the north side of the northern outlier on Creigiau Bychain ; BB.29048 from calcareous ash exposures west of the track on the north-east side of the central outlier of Rhiwlas Limestone on Creigiau Bychain.

Discussion. These two new species, representatives of which are fairly common in the ashes and limestones of the Gelli-grîn Group and in mudstones and sandstones of the Actonian Stage are the only examples of *Leptaena*, as understood by Spjeldnaes (1957 : 171), so far recorded from the Caradocian rocks of south Britain. Externally the most distinctive feature is undoubtedly the raised rim surrounding the ventral surface of the disc and representing a sharp, rounded, ventrally directed fold in the zone of geniculation. The average length of the disc in 20 pedicle valves of *L. ventricosa* was 9·2 mm. (variance 1·53) and its average percentage length relative to width in 4 pedicle valves was 63 (range 57–66). The values for 37 and 16 pedicle valves of *L. salopiensis* were respectively 13·0 mm. (1·757) and 62·4 (variance 70·47), and it is clear that in spite of similar outlines the disc of the Shropshire species is absolutely longer ($p < \cdot001$). There is also an important difference in ornamentation. The parvicostellate pattern is fairly coarse in both species with no conspicuous differential thickening of rounded costellae to define segments and 3, 4, 5 and 6 costellae per mm. were counted at 10 mm. antero-medianly of the umbo in 1, 7, 1 and 0 pedicle valves of *L. ventricosa* and 6, 17, 6 and 1 of *L. salopiensis*. The rugae, which are more or less symmetrical, are not invariably continuous in their concentric disposition because the earlier formed ones in particular may be interrupted by

saddles here and there. There is, however, a significant difference ($p < \cdot 01$) in the number of rugae displayed by both stocks for 4, 5, 6, 7, 8, 9, and 10 rugae ornament the discs of 1, 9, 11, 3, 2, 0 and 0 pedicle valves of *L. salopiensis* compared with 0, 0, 0, 3, 5, 4 and 1 valves of *L. ventricosa*. Hence the larger disc of *L. salopiensis* bears significantly fewer rugae but this is understandable in that the average wavelength of the fifth ruga antero-medianly of the umbo in 21 pedicle valves was 1·4 mm. (variance 0·058) whereas even the most distant rugae of *L. ventricosa* rarely attained a wavelength of 1 mm. Internally the two stocks are alike except for the less robust cardinal process, the less well developed notothyrial platform and the absence of striations on the teeth and sockets of *L. salopiensis* which differences are usually ascribed to excessive shell secretion and gerontism. The rhomboidal outline of the ventral muscle scar, for example is especially diagnostic for both species with an average percentage width relative to length of 89·0 (range 79–100) for 4 pedicle valves of *L. ventricosa* and of 85·0 (variance 290·5) for 13 valves of *L. salopiensis*. In summary then it may be said that despite many similarities, *L. salopiensis* is immediately distinguishable from *L. ventricosa* in its absolutely larger disc ornamented by fewer and coarser rugae.

The new species are most closely comparable with the type species of *Leptaena*, *L. rugosa* Dalman (see Spjeldnaes 1957 : 173) from the *Dalmanitina* beds and *L. veldrensis* Spjeldnaes (1957 : 179) from the *Coelosphaeridium* and *Mastopora* beds. From the former, however, both differ in the differently proportioned disc and the relatively longer and differently shaped ventral muscle scar and although they are like *L. veldrensis* in these features, the invariable presence of a rim to the ventral disc and the well defined pattern of rugation in both new species are reliable diagnostic differences.

Genus ***KIAEROMENA*** Spjeldnaes 1957

Type species. *Leptaena kjerulfi* Holtedahl by original designation of Spjeldnaes (1957 : 72).

Kiaeromena* cf. *kjerulfi (Holtedahl)

(Pl. 16, figs. 1–5, 8)

Description. Concavo-convex, weakly geniculate and relatively elongate *Kiaeromena* with a poorly defined disc between 11 and 15 mm. long, over four-fifths as long as wide and with a ventral depth of about one-fifth the length and subtending a rounded angle of about 100° with the trail to give an overall depth of over two-fifths the length of the pedicle valve ; radial ornamentation unequally parvicostellate with 5 or 6 costellae per mm., at 10 mm. antero-medianly of the ventral umbo ; 8 to 10 continuous, concentric asymmetrical rugae with wavelengths of about 1·5 mm. and steeper, shorter posterior sides also ornament the disc ; pseudodeltidium and larger chilidium well developed, foramen small, rarely closed, supraapical ; teeth small and widely splayed, continuous with short dental lamellae,

ventral muscle scar elongately oval, less than three-fifths as long as the disc and as wide as long in young valves but about four-fifths as wide as long in adult valves, adductor scars lanceolate, impressed anteriorly of a low median ridge and extending forwards for about three-fifths the length of the muscle field but not enclosed by the submedian lobes of the diductor scars ; cardinal process lobes long and slender, with a faint median ridge between them immediately below a slight indentation in the chilidium, notothyrial platform anchor-shaped with the lateral arms strengthening widely splayed socket ridges and together with the median ridge forming the posterior and median boundaries to a pair of subrounded dorsal adductor impressions that extend anteriorly for about one-third the length of the disc in young shells, slightly divergent submedian ridges within the dorsal adductor fields variably developed.

Material (Figured).	length	width (mm.)
Internal mould of pedicle valve (BB.29049)	21·0	23·0
Incomplete internal and external moulds of brachial valve (BB.29050–51)	—	—
Fragment of external mould of pedicle valve (BB.29052)	—	—
Internal mould of pedicle valve (BB.29053)	14·0	17·0
Internal mould of pedicle valve (BB.29054)	20·0	—

Horizon and locality. Allt Ddu Group : all specimens from fine sandstones and mudstones at the top of the Group and exposed in the north-west corner of the field 450 ft. south of Pandy-isaf Farm.

Discussion. The distinctive leptaenid *Kiaeromena* is fairly common in the highest Allt Ddu sandstones and siltstones although it is restricted to that horizon and the specimens are usually too deformed to permit more than a generic identification. Of all known species, however, the stock is closest to *K. kjerulfi* (Holtedahl) (see Spjeldnaes 1957 : 185) and, provisionally at least, must be regarded as conspecific with it. This is certainly true of ornamentation. Spjeldnaes emphasized the unequally parvicostellate nature of the Norwegian species and the prominence of the rugae, and the Bala specimens, with counts of 5 and 6 costellae per mm., 10 mm. antero-medianly of the umbones of 2 and 3 pedicle valves respectively and with 8, 9 and 10 rugae ornamenting the discs of 3, 3 and 1 pedicle valves, are indistinguishable. The relative proportions of shell and muscle fields, too, are comparable. Indeed the only differences appear to be the relative smallness of the pseudodeltidium and the comparative simplicity of the cardinal process lobes of Bala shells, but both these features have been studied in only a few moulds and, in any event, such differences might have been nothing more than gerontic effects in the larger Norwegian shells.

Genus *BELLIMURINA* Cooper 1956

TYPE SPECIES. *Leptaena charlottae* Winchell & Schuchert by original designation of Cooper (1956 : 854).

Bellimurina incommoda sp. nov.

(Pl. 16, figs. 6, 7, 10–14)

DIAGNOSIS. Elongately semi-elliptical plano-convex *Bellimurina* with pedicle valve between three-fifths and two-thirds as long as wide and just over one-fifth as deep as long at umbo ; radial ornamentation strongly unequally parvicostellate, with counts of 7 or 8 costellae per mm., at 10 mm. anterior of ventral umbo, and interrupted by fine, closely spaced, concentric lamellae to give a microscopic reticulate pattern, entire surface also rugate with rugae vaguely disposed concentrically at intervals of about 0·5 mm. but impersistent and broken by stronger costae and costellae ; ventral interarea apsacline, apical foramen very small, pseudodeltidium small, dorsal interarea anacline, chilidium large and arched ; teeth large, tetrahedral, striated and ankylosed to widely divergent dental lamellae, ventral muscle field well defined over one-third as long as pedicle valve, and slightly longer than wide, rhomboidal in outline with elevated boundaries becoming indistinct anteriorly ; pedicle callist well developed passing into broad, raised median ridge becoming narrow and low anteriorly where it separates a pair of lanceolate adductor scars not enclosed by anterior ends of flanking diductor scars ; cardinal process lobes, squat and well developed, standing above anchor-shaped notothyrial platform that is extended and curved laterally to fuse with widely divergent socket ridges, and prolonged anteriorly as low median ridge reaching forwards for less than one-half the length of brachial valve and separating a pair of suboval adductor scars, each further divided by a low submedian ridge.

		length	width (mm.)
HOLOTYPE.	Internal and external moulds of pedicle valve (BB.29055–56)	10·5	16·5
PARATYPES.	Internal and external moulds of pedicle valve (BB.29057–58)	—	—
	Internal and external moulds of brachial valves (BB.29059–60)	—	—
	Internal mould of brachial valve (BB.29061)	12·0	—

HORIZON AND LOCALITIES. Gelli-grîn Group : BB.29055–56 from calcareous ash crags exposed 650 ft. south-east of Bryn-briglas Farm ; BB.29057–60 from calcareous ashes exposed below the Rhiwlas Limestone scarp on the north side of the northern outlier on Creigiau Bychain ; BB.29061 from calcareous ash crags just south of the track leading west from Gelli-grîn Farm and 1,000 ft. west-south-west of the farm.

Discussion. Rare strophomenaceid moulds represent the first record of *Bellimurina* in the Lower Palaeozoic rocks of South Britain. There is no doubt about the affinities of the stock ; the internal features as well as the highly distinctive ornamentation, show its close relationship to American and Scottish congeneric forms. But, in spite of the few specimens collected, the new species is immediately distinguishable, in its plane brachial valve and well-defined rhomboidal ventral muscle scar, from all other known ones which invariably have a gently convex brachial valve with a tendency to become geniculate in a ventral direction, and a significantly wider muscle scar. Other differences like the absence of a dorsal sulcus or a regularly zig-zag rugate pattern constitute additional contrasts with *B. sulcata* Cooper (1956 : 858) from the Pratt Ferry formations of Alabama or *B. concentrica* Cooper (1956 : 856) from the Pierce formation.

Very little information concerning the morphological variability of the new species can be added to that already given in the diagnosis except with regard to two features. Thus the unequally parvicostellate ornamentation is strongly developed—the costellae appear to be segregated into segments up to 0·5 mm. wide, and counts of 7 and 8 costellae per mm. were obtained for 1 and 2 pedicle valves 10 mm. antero-medianly of the umbones. The rhomboidal ventral muscle scar is certainly less variable than one would expect because the average percentage length relative to the length of 6 internal moulds was 36·7 (variance 6·0) and the percentage width relative to length of 3 scars was 97, 94 and 84.

Superfamily RHYNCHONELLACEA Schuchert 1896

Family RHYNCHOTREMATIDAE Cooper 1956

Genus ***ROSTRICELLULA*** Ulrich & Cooper 1942

Type species. *Rostricellula rostrata* Ulrich & Cooper by original designation of Ulrich & Cooper (1942 : 625).

Rostricellula sparsa sp. nov.

(Pl. 16, figs. 9, 15–17)

Diagnosis. Broadly triangular in outline, almost four-fifths as long as wide with ventral apical angle of about 100°, unequally biconvex with brachial valve nearly two-fifths and pedicle valve about one-fifth as deep as wide, dorsal fold and ventral sulcus well defined, about two-fifths the maximum width of shell at strongly uniplicate anterior margin ; surface ornamented by narrowly angular costae with wavelength of 0·3–0·4 mm. on fold compared with 0·2 mm. on flanks at distance of 3 mm. from umbo ; two costae occupy the fold, with complementary median one in sulcus, and 4–6 finer ones occur on flanks ; dental lamellae fused with teeth, about one-seventh as long as pedicle valve, diverging at about 80° ; crural bases short, subtriangular in outline and not more than one-tenth as long as brachial valve, median ridge low but well defined represented externally by groove between submedian costae of dorsal fold.

		length	width (mm.)
Holotype.	Incomplete external and internal moulds of conjoined valves (BB.29039–40), dorsal aspect	3·5	4·0 (est.)
Paratypes.	Incomplete external and internal moulds of brachial valve (BB.28893–94)	—	4·2
	Incomplete internal mould of brachial valve (BB.28892)	3·3	—
	Internal mould of pedicle valve (BB.28977)	4·7	6·0

Horizon and localities. Allt Ddu Group : BB.29039–40, BB.28893–94 from mudstone crags cropping out 1,100 yds. east of Pant-yr-onen Farm ; BB.28892, BB.28977 from mudstones just north of road and 320 yds. east-south-east of Glynbach.

Discussion. Only five specimens of *Rostricellula* have been collected from the Caradoc rocks of the Bala district so that the quantitative estimates of various features given in the diagnosis, which never involve more than two specimens, are not important in the present systematic discrimination. The arrangement of the costae on the fold and in the sulcus is, however, highly distinctive. All American and the one known south British species of *Rostricellula* (*R. triangularis* Williams 1949 : 235) have at least two costae in the sulcus and three on the fold. Indeed only *R. ambigena* (Barrande) (see Havlíček 1961 : 51) from the Ashgillian of Czechoslovakia is comparable in the development of a costa in the sulcus and two costae on the fold. But these almost invariably bifurcate, or give rise by lateral branching to costellae, well within the size-range of the Bala specimens.

Superfamily SPIRIFERACEA Waagen 1893

Family CYCLOSPIRIDAE Schuchert 1913

Genus ***CYCLOSPIRA*** Hall & Clarke 1893

Type species. *Orthis bisulcata* Emmons by original designation of Hall & Clarke (1893 : 146).

Cyclospira sp.

(Pl. 16, fig. 18)

A few incomplete internal moulds of brachial valves belonging to the genus *Cyclospira* have been collected from the Gelli-grîn Group and one (BB.28976), from calcareous ashes exposed in the quarry beside the drive to Y Garnedd Farm and 300 ft. south-east of the farm, is described and figured here to give some idea of the salient features. The mould is 3·0 mm. long and evidently represented an elongately oval, gently convex valve lacking ornamentation but indented posteriorly by a shallow median sulcus which passes anteriorly into a low fold. The divided

hinge-plate, which extended anteriorly for about one-tenth the length of the valve, was about twice as wide as long. It consisted of a pair of robust, triangular crural bases slightly raised along their postero-lateral edges to define a pair of oval sockets and continuous along their inner edges with slender, rod-like crura. The crural bases were undercut and unsupported ; a thin, relatively high median septum originated just anterior of the hinge-line and extended anteriorly for about seven-tenths the length of the valve.

The valves are reminiscent of certain American *Cyclospira*, like *C. bisulcata* (Emmons) from the Trenton of New York State (see Cooper 1956 : 693), in the development of the fold anteriorly but until more is known of the species to which they belong, further comparison is unwarranted.

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